

# Optimising the trade-offs between food production, biodiversity and ecosystem services in the Neotropics



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This dissertation is submitted for the degree of  
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This thesis is dedicated to Katherine Claire Williams





## DECLARATION

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I hereby declare that except where specific reference is made to the work of others, the contents of this dissertation are original and have not been submitted in whole or in part for consideration for any other degree or qualification in this, or any other university. This dissertation is my own work and contains nothing which is the outcome of work done in collaboration with others, except as specified in the text and Acknowledgements. This dissertation contains fewer than 65,000 words including appendices, bibliography, footnotes, tables and equations and has fewer than 150 figures.

David Rhodri Williams

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## SUMMARY

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Agriculture is the greatest threat to biodiversity across the world and a major contributor to anthropogenic greenhouse gas emissions. Both pressures will increase over coming decades as populations and per capita consumption rise. How we choose to produce food will, to a large extent, determine the state of biodiversity and the wider environment in the 21<sup>st</sup> century.

Balancing livestock production and environmental concerns is of particular importance: rangelands cover approximately one quarter of the world's ice-free land and livestock consume over one third of all calories from crops. In addition, livestock, particularly ruminants are extremely inefficient and use more land, nitrogen and water than other foodstuffs, whilst producing more CO<sub>2</sub>. Finally, there is a strong relationship between wealth and meat consumption. Combined with increasing populations, this means that demand for meat is likely to continue to increase.

Two alternative strategies have been proposed to minimise the environmental cost of food production: land sharing attempts to maximise biodiversity within the farmed landscape by keeping yields artificially low. Alternatively, land sparing links high yield agriculture with increased habitat protection or restoration. Previous studies have examined the relative benefits of the two strategies in different agricultural systems and regions. However, my research is the first to look at a wide range of alternative livestock production systems in a highly disturbed part of the tropics.

To investigate this issue I collected data on the production and requirements of different cattle ranching systems in Yucatán, Mexico, as well as on the population densities of birds, trees and dung beetles, and carbon stocks in both natural habitats and the different ranching systems. I used novel methods to estimate the yields of my study sites and applied both previously developed density-yield functions and new scenario building methods to model how species and carbon stocks responded to increasing agricultural yields.

I found that all taxa, and carbon stocks, show similar responses: rapidly declining with conversion from natural habitats to agricultural land. The populations of most

species, and regional carbon stocks, were therefore maximised with a land-sparing strategy that combines high yields with forest protection or restoration.

Such a strategy is broadly aligned with the goals of producers, environmental organisations and policy makers in Yucatán. However, mechanisms for active land sparing, which can link yield increases with habitat protection, will be needed to ensure that the benefits of land sparing can be realised. In addition, even with land sparing, probable 2030 production targets still resulted in forest loss, highlighting the need for demand reduction as an important part of a sustainable food strategy.

## ABBREVIATIONS AND GLOSSARY

---

AIC	Akaike's Information Criteria, a measure of the relative quality of a model's fit
AICc	AIC corrected for small sample sizes
C	Carbon
CO <sub>2</sub>	Carbon dioxide
CONABIO	Comisión Nacional para el Conocimiento y Uso de la Biodiversidad – the Mexican National Commission for the Knowledge and Use of Biodiversity
dbh	Diameter at breast height, diameter at 1.3 m from the ground — a standard measure of tree diameter
Dressing percent-age	The ratio of carcass weight to live weight for livestock, a measure of the amount of edible meat in an animal
EOO	Extent of Occurrence. A measure of the global range of a species, used by e.g. BirdLife International
GPS	Global Positioning System
ha	Hectare (100 x 100 m)
INECOL	Instituto de Ecología – the Institute of Ecology, Xalapa, Veracruz, Mexico
INEGI	Instituto Nacional de Estadística y Geografía. – the Mexican National Institute for Statistics and Geography
ISPS	Intensive Silvopastoral Systems, a livestock production system combining pastures with banks of protein-rich legumes such as <i>Leucaena leucocephala</i> planted at high densities
IUCN	International Union for the Conservation of Nature
km	Kilometer. 10 <sup>3</sup> metres
kg	Kilogram. 10 <sup>3</sup> grams
m	Metre

Mg	Megagram. $10^6$ grams, 1000 kg, or 1 tonne
N	Nitrogen
PROGAN	Producción Pecuaria Sustentable Ordenamiento Ganadero y Apícola – Programme for the Sustainable Production and Management of Livestock and Beekeeping, a Mexican subsidy programme to support smallholder ranchers
REDD	United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation in Developing Countries
SAGARPA	Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación – the Mexican agricultural ministry (literally “The Secretariat of Agriculture, Livestock, Rural Development, Fisheries and Food)
t	Tonne. 1000 kg
TD	Tizimín District in the north of Yucatán State, Mexico
UADY	Universidad Autónoma de Yucatán – Autonomous University of Yucatán, based in Mérida, Yucatán
UNAM	Universidad Nacional Autónoma de México – Autonomous National University of Mexico, based in Distrito Federal
US	United States of America
USFDA	Food and Drug Administration of the United States of America
YP	Yucatán Peninsula, a region comprising the Mexican states of Yucatán, Quintana Roo and Campeche, as well northern parts of Belize and Guatemala



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Ferruginous pygmy owl *Glaucidium brasilianum*



## INTRODUCTION

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*“If we fail on food, we fail on everything”*

Charles Godfray

### 1.1 Agriculture and the environment

The decisions we make about what food we eat and how we produce it will have profound consequences for humanity and the environment. Agriculture is perhaps the most important single activity for human welfare; providing almost all the food we eat and supporting billions of people’s livelihoods, particularly in developing countries (FAO, 2015). However it also has a huge environmental impact: it threatens more species (Dirzo and Raven, 2003; Green et al., 2005) and uses more water (Shiklomanov, 2000; Rost et al., 2008) than any other sector and contributes 12–35% of global greenhouse gas emissions, largely through land-use change, but also from fossil fuel use, fertiliser production and methane emission from rice paddies and ruminant digestion (Houghton et al., 2001; Gibbs et al., 2007; van der Werf et al., 2009; Defries and Rosenzweig, 2010).

The loss of biodiversity is concerning for its own sake, as future generations will inherit an increasingly impoverished natural world, but biodiversity is also hugely important for human wellbeing. More biodiverse ecosystems are likely to be more resilient and use resources more efficiently (Tilman et al., 2014) and the services that ecosystems provide regulate the climate, support agriculture and provide huge cultural benefits (Balmford et al., 2002; Karp et al., 2013; Costanza et al., 2014). In addition, the genetic resources of wild biodiversity are likely to be vital in ensuring the long-term sustainability of food production (Fowler and Hodgkin, 2004) as well as providing

a large proportion of medical drugs (Bernstein and Ludwig, 2008). Greenhouse gas emissions from agriculture are also linked to human wellbeing: the climatic change brought about by increasing greenhouse gas concentrations may reduce agricultural yields (Schlenker and Roberts, 2009), affect human health (Patz et al., 2005) and could even render regions of the world uninhabitable (Pal and Eltahir, 2015). Balancing food production with environmental concerns is therefore arguably the biggest challenge facing humanity in the 21<sup>st</sup> century.

This challenge will become more acute as populations and per capita consumption continue to rise. If current trends are maintained then global agricultural production will have to increase by 50–100% to keep pace with demand (The Royal Society, 2009; Tilman et al., 2011). This is not, however, a normative target (Tomlinson, 2013) and there are many ways that demand can be reduced: we currently waste one third of food (Gustavsson et al., 2011) and feed 36% of the calories produced by crop plants to livestock; a far less efficient way of using production than direct consumption. In addition, perhaps two billion people consume more than is healthy, even as another billion go hungry (Burlingame and Sandro, 2012)

Tackling these demand-side issues could greatly reduce environmental pressures, but there will always be more and less harmful ways of producing food, irrespective of the overall level of production. Agriculture is also not a uniform entity across the world. Labour intensive, and often low yield, subsistence farming supports huge numbers of people, particularly in poorer countries, whilst fossil fuel intensive and heavily mechanised agriculture is found across North America and Europe (Ramankutty and Foley, 1998; Ramankutty et al., 2008; FAO, 2015). In addition, large areas, particularly in the tropics, are under some form of rotational agriculture: so-called slash-and-burn, or swidden farming (Van Vliet et al., 2012). Finally, low precipitation regions across the world support nomadic or low intensity pastoral systems, which in total cover more area than any other land use (Reid et al., 2008).

Each of these broad agricultural systems contains a wide range of agricultural practices with variable environmental impacts. To minimise the negative impacts of agriculture requires an understanding of how different aspects of farming systems affect the environment. One fundamental question is how we balance the on-farm and off-farm impacts of agriculture, and it is this question that my thesis addresses.



## 1.2 Balancing food production and the environment: land sparing and land sharing

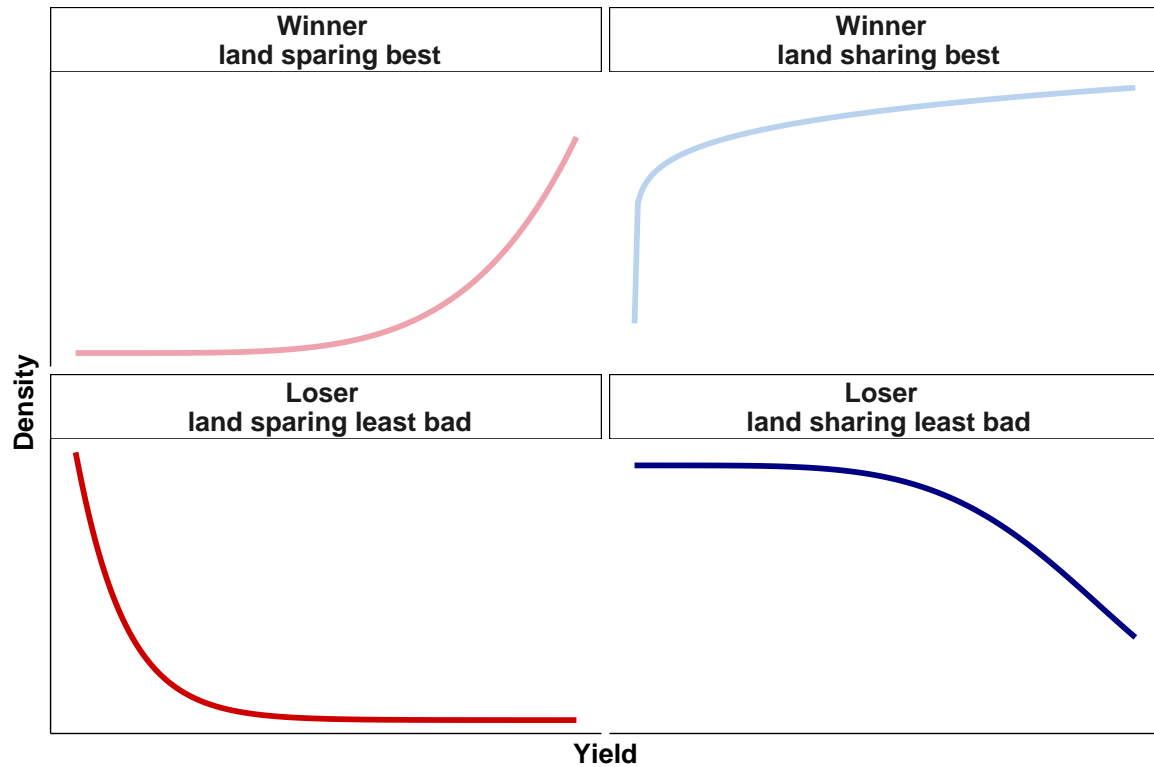
### 1.2.1 Conceptual background

Agricultural systems are hugely complex ecological, social and economic systems (Fischer et al., 2014). Investigating one or two aspects of this complexity can provide information on the relative impacts of different strategies, but only if the most informative variables are investigated.

Agricultural yield is a key determinant of environmental impact. Increasing yields can reduce on-farm biodiversity (Donald et al., 2001) by reducing the primary production available for other species, reducing non-crop habitats, or increasing pesticide and herbicide use (e.g. Chamberlain et al., 2000; Benton et al., 2003). However, higher yields reduce the area required to produce a given amount of food, potentially freeing up land for the conservation or restoration of natural habitats.

Two broad strategies for balancing agriculture and environmental concerns can therefore be imagined. The first aims to minimise the on-farm impacts of agriculture using measures that often reduce yields. For example, European Union agri-environment schemes have included measures to increase non-crop habitat, take land out of production, or reduce pesticide use (Natural England et al., 2015). In extremis, this strategy is termed land sharing and involves farming all available land at the lowest possible yields to maximise on-farm biodiversity. Alternatively, an extreme land sparing strategy produces food at the highest sustainable yields, thereby sparing as much land as possible for conservation. Between these extremes there are many intermediate yield strategies.

Which strategy is the least damaging to nature will depend on how species and ecosystem services respond to increasing yields. The relationship between a species' population density and yield can be described using density-yield functions, the shape of which can be used to categorise species into those that win or lose under agriculture and those which are favoured by different land-use strategies (Fig. 1.1, Green et al., 2005). This approach can be usefully complemented by building and parameterising land-use scenarios for estimating species population size under different strategies (Edwards et al., 2014; Gilroy et al., 2014b; Edwards et al., 2015). Generally, species that decline rapidly as natural habitats are converted will do least badly with a land-sparing strategy that maximises natural habitat conservation, whilst those decline more slowly will do least badly with land sharing.



**Fig. 1.1** Typical density-yield functions for species that respond differently to agricultural yields. Other curve shapes are possible — for example some species’ population densities first increase and then decrease as yields increase.

### 1.2.2 Previous work and knowledge gaps

Many studies have investigated the environmental impacts of different agricultural systems to identify the least harmful, with very little consensus (e.g. Edwards et al., 2010; Phalan et al., 2011b; Wright et al., 2011; Clough et al., 2011; Hulme et al., 2013; Gilroy et al., 2014b; Mastrangelo and Gavin, 2014; Dotta et al., 2015). Whilst there may be genuine differences between farming systems and regions, confusion can also arise from the use of different metrics for both biodiversity and agriculture (Phalan et al., 2011a). Species richness is often used as a measure of biodiversity (e.g. Steffan-Dewenter et al., 2007; Clough et al., 2011; Mastrangelo and Gavin, 2012) but does not include information on either species identity or the probability of individual species’ persistence; focusing on a subset of species or habitats such as farmland birds, or not comparing all possible land uses in a system in will also make it difficult to draw meaningful conclusions (e.g. Smith et al., 2010; Verhulst et al., 2004). Meanwhile, using metrics other than yield, or comparing strategies without controlling for overall levels of production, may underestimate the environmental impacts of low yield agriculture.

Studies that have investigated how the population sizes of all species in a taxon respond to changing yield have overwhelmingly found that, for a given level of agricultural production, land sparing allows more species to maintain larger populations than any other land-use strategy (Phalan et al., 2011b; Hulme et al., 2013; Edwards et al., 2014, 2015; Dotta et al., 2015; Kamp et al., 2015; Feniuk, 2016). The few studies to examine ecosystem services under different land-use strategies have also found that land sparing is likely to allow for greater retention of carbon stocks at most levels of production (Wade et al., 2010; Gilroy et al., 2014b). In addition, land sparing could considerably reduce land-use change and greenhouse gas emissions at a regional and global scale (Foley et al., 2011; Tilman et al., 2011; Lamb et al., 2016a).

Despite the strength of these findings, biodiversity in other regions and agricultural systems may respond differently. In particular, a long history of disturbance may act as an extinction filter, leaving behind a biota with fewer sensitive species, which is more resilient to agriculture (Balmford, 1996), and hence more likely to fare better under land sharing. The different ecological characteristics of livestock production may also mean that species respond differently to increasing yields.

Understanding the least damaging way to produce livestock is of particular importance because of their vast environmental impact. Rangelands cover 28–34 million km<sup>2</sup> (22–27% of the Earth’s ice-free surface, Ramankutty et al., 2008; FAO, 2015), more than any other land use and nearly twice the area under cropland. Production of meat, particularly ruminant meat, results in far greater greenhouse gas emissions and uses more land, water and reactive nitrogen than any other foodstuff, whether measured per calorie, per gram or per serving (Eshel et al., 2014; Tilman and Clark, 2014). Furthermore, there is strong relationship between wealth and meat consumption (Tilman and Clark, 2014), and as both population and per capita income continue to increase, meat demand is also rising quickly (Fig. 1.2, FAO, 2015).

Investigating livestock systems typically requires new forms of analyses. Animals are often moved from low yield breeding areas to higher yield finishing systems and receive fodder that may be produced off-farm. Understanding and modelling these more complex systems and their impacts is an important step towards more holistic analyses that incorporate the growing complexity of food production systems.

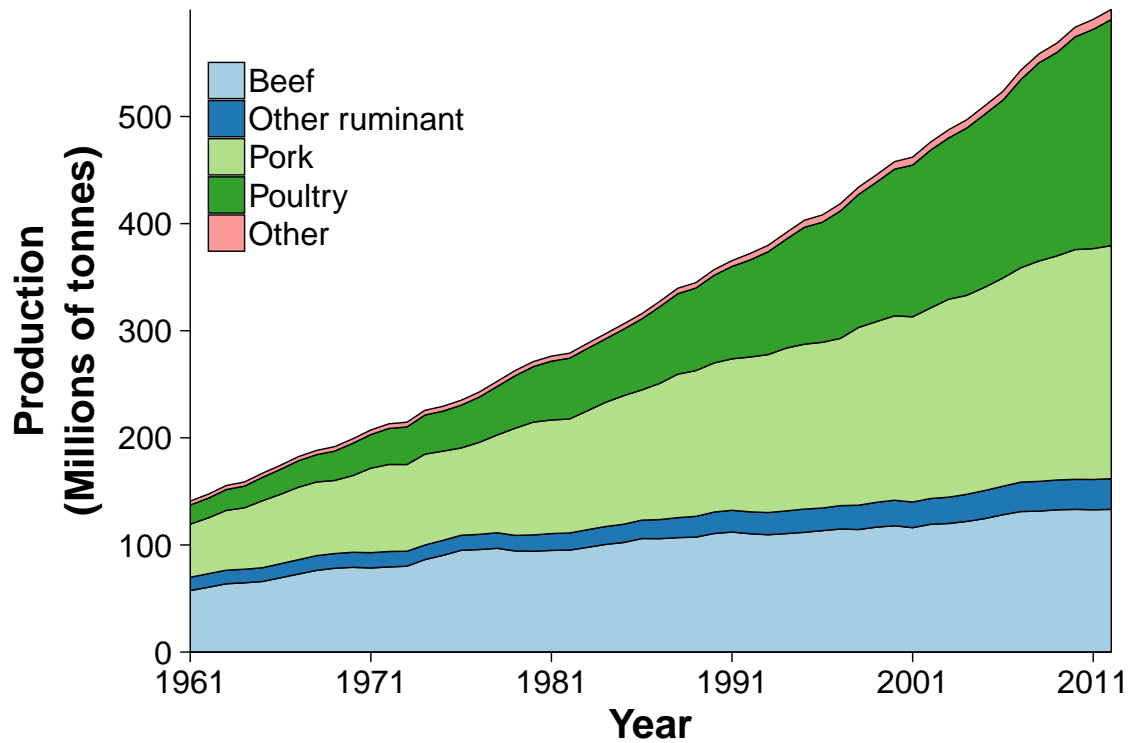


Fig. 1.2 Global meat consumption patterns for 1961–2012. Data from FAO (2015)

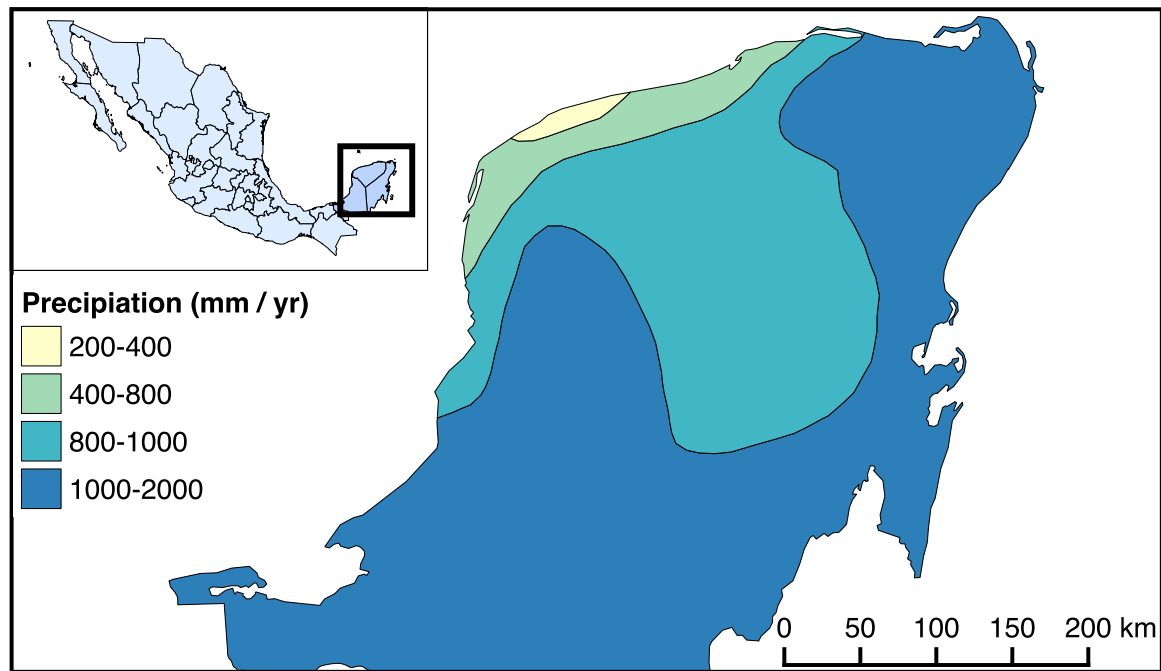
### 1.3 Study system and study region

To contribute to the debate on reducing the environmental impact of food production I therefore decided to investigate livestock production in a part of the world with long history of disturbance: the Yucatán Peninsula (YP) in southeast Mexico.

#### 1.3.1 The ecology of the Yucatán Peninsula

The YP comprises extremely porous karstic limestone bedrock, deposited over the course of 100 million years and resulting in a uniformly flat topography with no rivers (Vázquez-Domínguez and Arita, 2010). Soils are thin but have very high nitrogen and carbon contents (Benjamin et al., 2001; Weisbach et al., 2002) and can vary over short distances, resulting in a mosaic of different types (CONABIO, 1995).

The YP's climate is predominantly 'tropical wet and dry' (Aw in the Köppen Climate Classification, CONABIO, 1995), but with strong temperature and rainfall gradients: from hot and dry in the northwest to relatively cool and wet in the southeast (Fig. 1.3). Vegetation types follow this gradient, from tropical dry forests to tropical



**Fig. 1.3** Precipitation rates in the Yucatán Peninsula and the Peninsula's position within Mexico. Data from CONABIO (1995).

evergreen forests. The forest has expanded and contracted with climatic changes and savanna systems occupied much of the peninsula during parts of the Holocene (Hodell et al., 1995; Haug et al., 2003; Vázquez-Domínguez and Arita, 2010). The region is also subject to frequent hurricanes that can have extreme, although largely short-term, effects on vegetation and other taxa, and which may have been more frequent in the past (Liu, 1999; Liu and Fearn, 2000; Allen and Rincon, 2003). Other species are likely to have followed these long and short-term vegetation changes and many bird species also show seasonal movement: tropical-forest species expand their ranges in cooler and wetter months and years, retreating again as conditions deteriorate (Paul Wood, *pers. com.*). This dynamic environment makes the region well-suited for investigating the impacts of evolutionary and ecological history on species' sensitivity to contemporary land-use change.

### 1.3.2 The history and future of land use in Yucatán

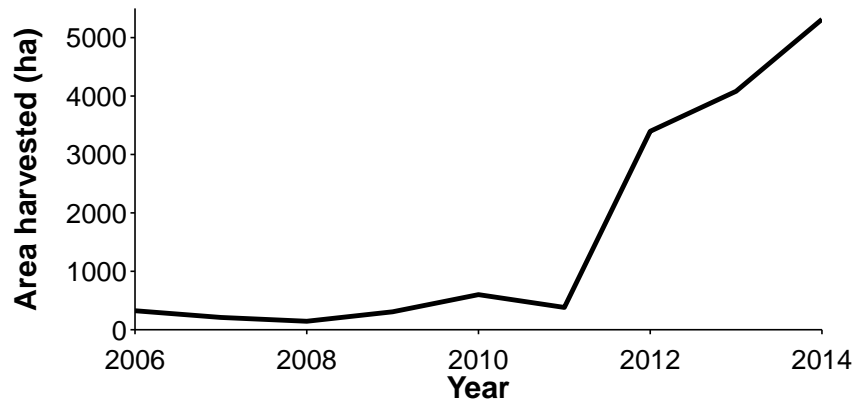
The YP also has a long history of anthropogenic modification, beginning with the cultivation of maize (*Zea mays*) and the expansion of the Pre-Classic Mayan civilisation (1000 BCE – 250 CE). At its height, the Classic Mayan (250–900 CE) population numbered in the millions and although the exact environmental impact of the Mayans

is debated (Gómez-Pompa and Kaus, 1999; Allen and Rincon, 2003), it is certain that there was extensive clearing of vegetation for agriculture for centuries. After the Mayan collapse and Spanish conquest, the region's population fell and natural vegetation recovered (Gómez-Pompa and Kaus, 1999). In the 19<sup>th</sup> century, land was again cleared for *sisal* (*Agave sisalana*) and *henequen* (*Agave fourcroydes*) cultivation before this industry also collapsed (Gonzalez-Iturbe et al., 2002). Finally, the mid and late 20<sup>th</sup> century saw the rapid expansion of cattle ranching (Busch and Vance, 2011). This history has left very little, if any, original vegetation in the YP, but there is also no evidence of major floristic change over the past six thousand years (Gómez-Pompa and Kaus, 1999), supporting the idea of a relatively resilient biota.

Cattle ranching is now the dominant land use in the north of the YP (CONABIO, 1995) with most production specialised into three linked ranch types. Breeding ranches produce calves, raise them to 180–220 kg and sell them for export or to finishing ranches, which fatten the animals to a slaughter weight of 450–550 kg. Both rely on fodder as well as grazing land - largely maize, which is produced in the region in specialised maize ranches but also imported. Rarer are *completo* ranches, which combine breeding and finishing production: both breeding animals and rearing them to slaughter weight.

Land uses and management practices vary across ranches, resulting in four broad categories: traditional, *tecnificado*, silvopastoral and maize ranches. Traditional ranches are dominated by pastures of introduced African grasses such as *Panicum maximum* and *Brachiaria brizantha*. The thin soils mean these pastures are low yielding, and producers often graze animals in forests or secondary regrowth to provide shade and fodder in the dry season (although only rarely do they promote fodder plants such as *Brosimum alicastrum* or *Leucaena leucocephala*). To increase yields some producers 'mechanise' their pastures: breaking up and removing the underlying rock and importing earth to increase the depth and quality of the soil. In *tecnificado* ranches, mechanisation may be combined with irrigation, high rates of fodder use and intensive cattle management. Intensive silvopastoral systems have recently been promoted as a more sustainable way to increase yields by combining mechanised pastures with banks of protein-rich legumes, such as *Leucaena leucocephala*. Such systems can greatly increase yields (Mannetje, 1997; World Bank, 2008; Broom et al., 2013) and have been promoted as beneficial for ecosystem service provision and biodiversity conservation (Dagand and Nair, 2003; Broom et al., 2013). Finally, the area of mechanised and irrigated maize in northeast Yucatán has increased rapidly since 2011 (Fig. 1.4), probably because of rising maize prices driven by the diversion of US maize to bioethanol production

(Wise, 2012). Ranches of all types also have areas of fodder grass such as *Pennisetum purpureum* used both fresh and as hay or silage.



**Fig. 1.4** Area of irrigated maize in Tizimín District, 2006–2014 (SAGARPA, 2015). Most irrigated maize in the region is used for cattle fodder (*pers. obs.*).

## 1.4 Aims of this thesis

In this thesis I investigate which agricultural strategies will do the least harm to biodiversity and carbon stocks in the Yucatán Peninsula, expanding the land sparing/land sharing framework to a highly disturbed region of the tropics and to a complex agricultural system. To do this I:

- Collected data on agricultural yields, population densities of birds, trees and dung beetles, and carbon stocks for a range of ranch types (Chapter 2).
- Developed novel methods to estimate the yields of livestock production systems (Chapter 3).
- Investigated how biodiversity and carbon stocks respond to increasing livestock yields in a region with a long history of disturbance (Chapters 4 and 6).
- Created plausible land-use scenarios that contain multiple interdependent land uses (Chapter 5).
- Used these scenarios to estimate the impacts of different agricultural strategies on regional-wide species' populations and carbon stocks (Chapters 5 and 6).





## CHAPTER 2

### GENERAL METHODS

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*“At first blush I am tempted to conclude that a satisfactory hobby must be in large degree useless, inefficient, laborious, or irrelevant.”*

Aldo Leopold – *A Sand County Almanac*

## Introduction

The purpose of this chapter is to describe the methods I used to select study sites and collect the quantitative data on agricultural yields, biodiversity and carbon stocks that I have used in my analyses. Many of these data are used in multiple chapters, so I will avoid repetition by detailing my methods here.

## 2.1 Study site selection and mapping

### 2.1.1 Introduction

To investigate the impacts of different agricultural systems on biodiversity and ecosystem services I required samples representative of all feasible local agricultural systems, as well as zero-yielding natural habitats. I matched sites for key biophysical characteristics such as climate and soil type and wanted my sites to be comparable to those in other studies of this kind (e.g. Phalan et al., 2011b; Hulme et al., 2013; Feniuk, 2016).

## Overview of Yucatecan landscape

There is very little old growth forest remaining in the Yucatán Peninsula (YP) and much of the north and east of the peninsula is now under cattle pasture of different types. As Chapter 1 describes, these ranches can be managed as traditional pastures, silvopastoral ranches or *tecnificado* ranches. In addition, I needed to sample remaining natural habitats, and specialised maize ranches. I therefore selected five types of study site: zero-yielding natural habitats, traditional ranches, silvopastoral ranches, *tecnificado* ranches and maize ranches.

## Site design

I used 1 km<sup>2</sup> squares as my study sites. These are large enough to be biologically relevant and to capture the heterogeneity within landscapes. I chose to sample landscapes rather than landholdings to avoid potential biases from studying ranches of only one size class, or systematically under-sampling habitats such as hedges which are found mostly on property borders.

To minimise edge effects I sought study sites with a 500 m buffer similar habitat. To ensure independence I also sought study sites at least 5 km from sites of the same type and 1 km from any other site. However, this did not always prove possible (see Section 2.1.2).

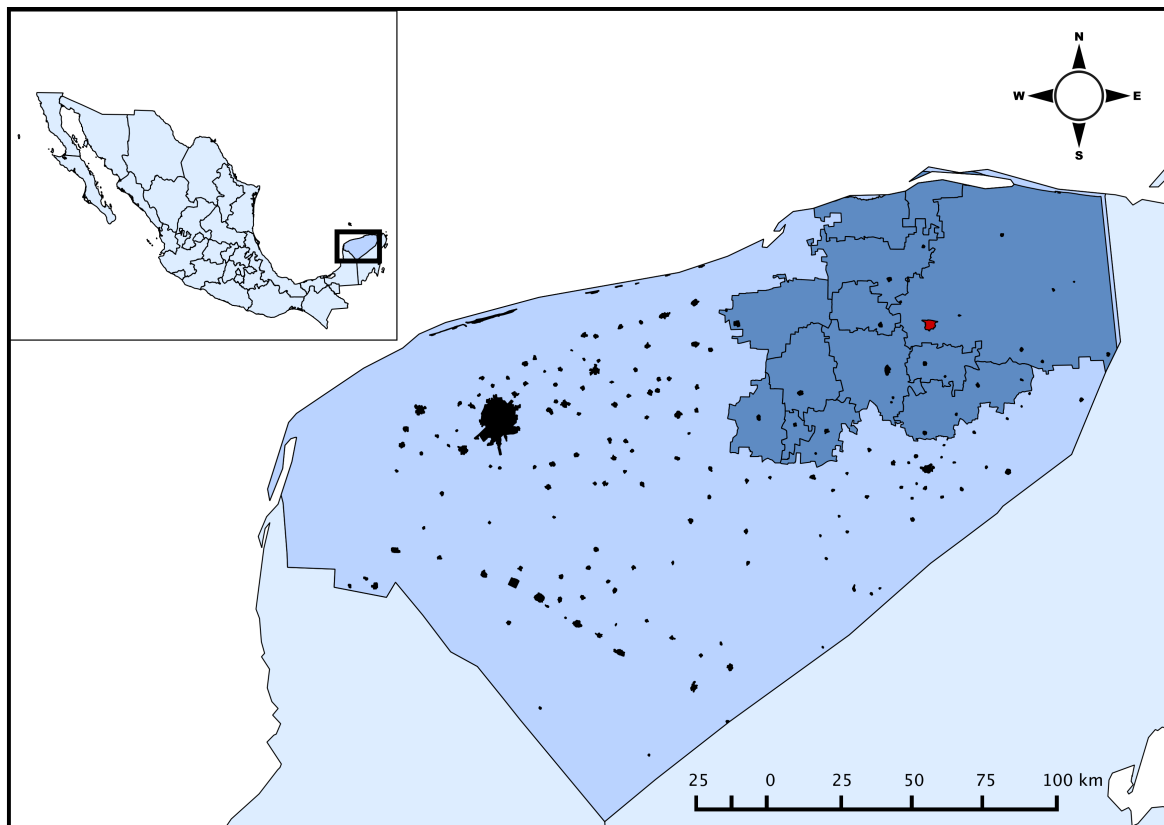
## Ensuring study sites were representative

To control for regional gradients in temperature and precipitation (Fig. 1.3) I restricted my study region to Tizimín District (TD) in the northeast of Yucatán State (Fig. 2.1). This region is the centre of cattle ranching in the peninsula and has been identified as a region with a large number of threatened plant species, but few terrestrial protected areas (Tetetla-Rangel and Durán, 2012). I distributed my sites across the major soil types present. TD has uniform topography and no rivers, so I did not have to control for these factors.

## 2.1.2 Site selection methods

### Traditional ranches

Using QGIS (QGIS Development Team, 2015) I placed a 1 km grid across a soil map across TD (CONABIO, 1995) and used Google Earth (Google Inc., 2015) to find areas that represented the range of vegetation types found in traditional ranches: grazed



**Fig. 2.1** Location of TD (dark blue) within the state of Yucatán (mid-blue), and Yucatán within Mexico. Towns are shown in black, with Tizimín town in red. Data from CONABIO (2015)

forest; mosaics of forest, regrowth and pasture; and open pastures. I randomly selected 10 grid squares from each vegetation type and visited them to check that land uses matched satellite imagery and to speak to land owners. If land uses had changed, if the site was within 500 m of ungrazed forest or secondary vegetation, or if I was not able to speak to the owners, then I moved to the next potential square.

### Other ranch types and baseline sites

The other productive site types are rare in the region, meaning I had to select almost all available sites, irrespective of location. I found sites by talking with ranchers, experts from the Universidad Autónoma de Yucatán (UADY), the agricultural ministry (SAGARPA) and the local *ganadería* (livestock) association in Tizimín. Once I had located potential sites I visited them to check land uses and to meet the owners.

I found potential baseline sites by talking to local ecologists and conservationists and identifying large areas of forest using Google Earth. I then visited potential sites to talk to owners and to assess their suitability.

### Obtaining permission to work in sites

To obtain permission to work in potential study sites I visited each landowner or manager in a site to explain my project, the data I required, and my fieldwork plans. One baseline site was located on communally owned *ejido* land, so I visited the local *comisarios*, explained my project, and obtained permission from the community to work there. Across all the ranches I visited, just one producer refused access, although a second manager withdrew permission to access their land in my final field season.

### 2.1.3 Mapping sites

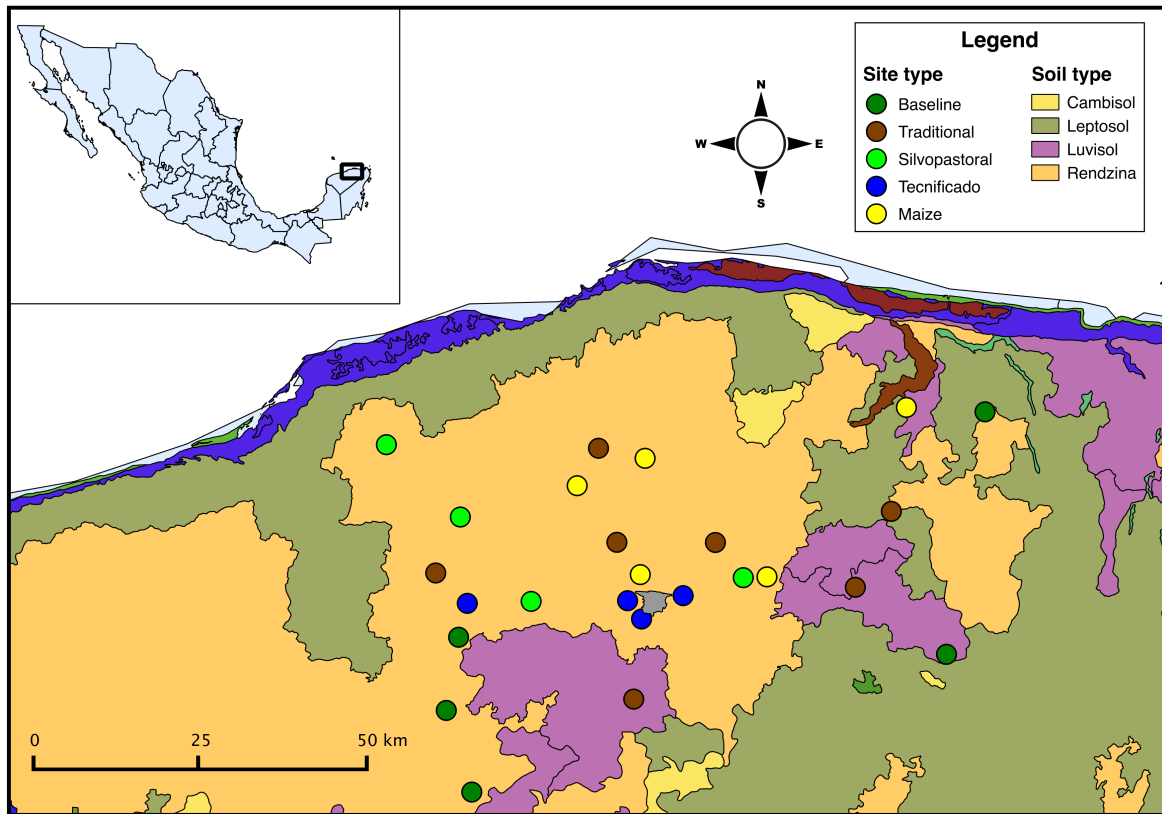
Except for the randomly located traditional ranches, I used Google Earth to position study sites and maximise coverage of the land use of interest. I then mapped them using Google Earth and site visits.

### 2.1.4 Results

#### Sites selected and land uses present

The locations of the selected sites selected are shown in Fig. 2.2, with the coverage of different land uses in Fig. 2.3.

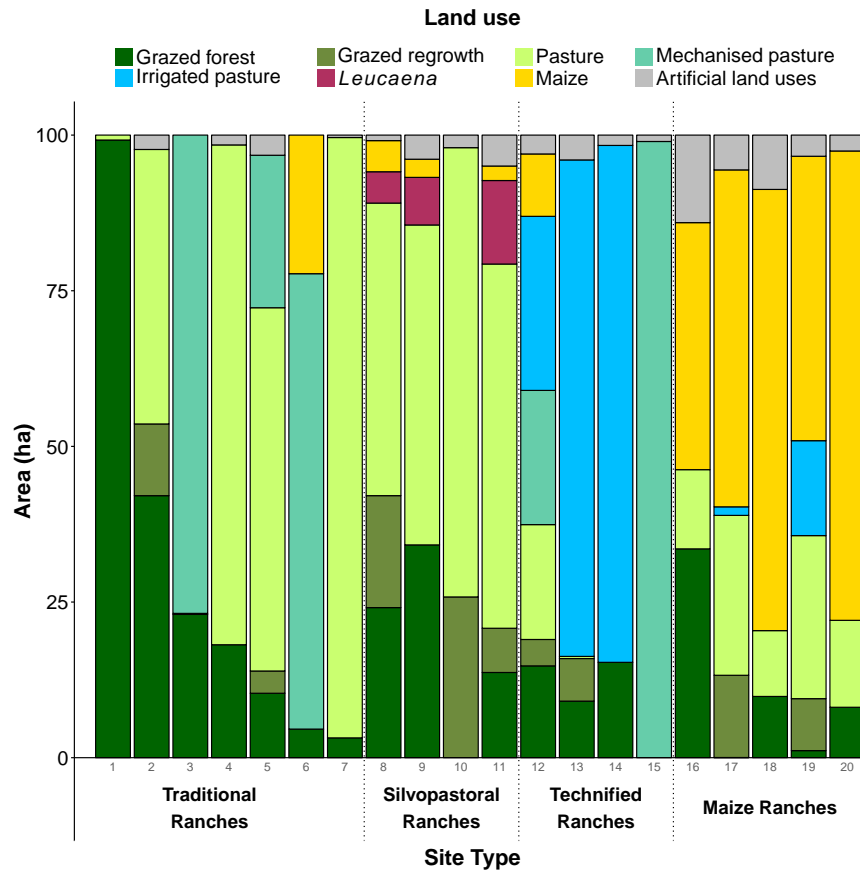
- **Baseline sites:** four of the five sites had large areas of forest over 30 years old; the fifth site had only been converted from a productive ranch approximately 15 years previously. Three of the sites (including the youngest) were actively managed: two private ranches had government-sponsored reforestation programmes in some areas and the *ejido* site contained some *milpa* agriculture (although my 1 km<sup>2</sup> study site did not). Some hunting and timber extraction occurred in all sites. These factors mean that the biodiversity and carbon storage values of my baseline sites may be lower than for older forest (Barlow et al. 2007; Eaton and Lawrence 2009, but see Smith et al. 2001). My results may therefore give conservative estimates of the benefits from land sparing but, on the other hand, provide realistic estimates for the short- and medium-term benefits of habitat conservation or restoration.



**Fig. 2.2** Position of 1 km<sup>2</sup> study sites within study region. Soil map is taken from CONABIO (1995). Tizimín town is shown in grey.

- **Traditional ranches:** seven sites with a wide range of land uses from grazed forest, to large expanses of extensive pasture and areas of mechanised or irrigated pasture (Fig. 2.3). The sites also differed in the intensity of animal management. Through observing over 100 ranches during my fieldwork, I feel these sites captured a large amount of the variation in traditional cattle production in the region.
- **Silvopastoral ranches:** three sites had intensively managed *Leucaena leucocephala* plantings, but these made up <20% of all sites, reducing my ability to investigate the impacts of this land use. The fourth site held a much larger area of silvopasture (>70%), but this was not intensively managed in the same way.
- **Tecnificado ranches:** all four sites contained large amounts of irrigated or mechanised pasture with intensive management of pastures and animals, including rotational grazing at high stocking densities, large fodder inputs and the frequent application of supplements, antihelminthics, and other medicines.

- **Intensive maize ranches:** all five sites contained large areas of maize but also pasture, unproductive land, fodder grass and irrigated pasture. Some practised crop rotation and several of the ranches replaced areas of pasture with additional maize fields during my field seasons.



**Fig. 2.3** Areas of different land uses within my final 20 productive study sites.

## 2.2 Yield questionnaires

### 2.2.1 Introduction

Here I describe the protocol for interviewing producers and the initial data processing. The more complex yield estimation methods are in Chapter 3.

## 2.2.2 Methods

### Locating producers

As I explain in Chapter 3, modelling the yields of individual land uses required a larger sample size of ranches than were found in my study sites. I began by interviewing producers who had ranches within my study sites and then used a combination of *ad hoc* and targeted ranch visits, as well as visits to local *ganadería* associations and livestock fairs, to talk to more producers.

I interviewed producers with a wide range of ranch types and land uses; with ranches of varying sizes; and with ranches distributed across TD. I assessed data as I collected it and asked producers and other local experts to help locate undersampled ranch types. I also used a bootstrapping approach to judge when I had sampled enough ranches to have confidence in my modelled yield estimates (Chapter 3, Section 3.2).

### Interview protocol

In each ranch I identified the person (or people) I needed to talk to and made sure they had permission from the owner or manager to talk to me. I started by explaining who I was, what my research was about, and my affiliations with the University of Cambridge, Universidad Autónoma de México (UNAM), and UADY. I explained that the data would only be seen by me and would be anonymised and that I was not affiliated with, and would not pass data on to, the government. If producers were not comfortable in sharing their information I thanked them for their time and moved on to the next ranch. Most ranchers, however, were proud of their ranches and very happy to talk to me.

For ranches outside my study sites I kept interviews as brief as possible and asked for information on:

- The area of different types of grazed land use (pasture, mechanised pasture, irrigated pasture, grazed forest and grazed secondary regrowth) in their ranch.
- The number and weight of animals (cows, calves and other livestock) bought each year.
- The number and weight of animals sold each year.
- The yields of any fodder crops, including fodder grass, grown on the ranch.
- The weights of different fodders used by the ranch each year. If feeding regimes varied throughout the year then I asked for estimates for all months or seasons.

- The costs of any purchased fodder.

I also conducted longer interviews with producers inside my study sites, asking for additional information on:

- The costs of animals bought and sold.
- Capital, maintenance and running costs for mechanised and irrigated pastures.
- Labour costs.
- Timings and costs of vaccinations, medicine applications and veterinary visits.
- Transaction costs of buying/selling animals (mainly transport to and from the ranch).
- Miscellaneous costs such as fence maintenance, vehicle purchase, fuel costs etc.
- Subsidies received.

For both interview types, I asked for as many years of data as the interviewee could recall.

### **Data processing: Data cleaning**

Some interviewees gave very unusual answers such as extremely high maize yields. On these occasions I asked for clarification, but once or twice I still felt that the answers were unfeasible and discarded the questionnaire data for that ranch. I also discarded interviews when interviewees could not recall all the information, unless it was data on ranch economics or fodder crop yields.

### **Data processing: Standardising currencies**

To compare sites I converted inputs and production into universal currencies. I converted fodder inputs into “maize equivalents” based on metabolisable energy, which is the most commonly limiting factor in Yucatecan ranches (Baba, 2007). I converted fodder mass into joules and divided by the energy content of maize grain (Table 2.1). I could not identify the energy content of some pre-mixed fodders, so assumed they had an energy content equivalent to maize grain. I converted production of animal products into kilograms of edible protein using a dressing percentage of 50% (FAO, 1972) and a protein content of ruminant meat of 17.4% (USFDA, 2015). When ranches produced milk I converted volumes to masses at  $1.03 \text{ kg l}^{-1}$ .



**Table 2.1** Fodders used in ranches, their metabolisable energy content for ruminants and the ratio of this to the energy in maize grain. Values are from Animal Feed Resources Information System (2014) and given for dry weights.

Fodder	Energy content (MJ kg <sup>-1</sup> )	Maize Equivalents
Maize grain	13.7	1
Bran	11.2	0.817
Bread	11.2	0.817
Canola	11.3	0.828
Chicken litter	9.1	0.667
Fodder grasss	8.1	0.593
Maize silage	10.8	0.789
Molasses	9.6	0.703
Oats	11.8	0.864
Rice husks	3.0	0.220
Sorghum grain	13.5	0.989
Sorghum silage	8.4	0.615
Soy meal	13.6	0.996

### 2.2.3 Results

I was able to interview representatives from 35 of the 36 ranches within my study sites and 92 producers in total. I excluded five for the reasons above. Another 10 were from *completo* ranches which did not provide a large enough sample to model their yields separately (see Chapter 3). Of the 77 remaining interviews, 49 were from breeding and 28 from finishing ranches. Very few producers had intensively managed *Leucaena* in their ranches, so I combined this land use with irrigated pastures for further analyses.

## 2.3 Biodiversity surveys

Here I report the methods I used for collecting data on birds, trees and dung beetles. Dung beetles were surveyed by my colleague Fredy Alvarado from the Instituto de Ecología (INECOL) in Xalapa, and identified by Fredy and Fernando Escobar (also at INECOL). Fredy is kindly allowing me to report on his findings, but all credit for the collection of these data are due to Fredy and Fernando.

### 2.3.1 Introduction

Target taxa had to meet certain criteria. They had to be:

- Practical to survey across 25 study sites in a relatively short time.

- Found across the whole range of study sites.
- Show a variety of responses to habitat alteration and agriculture.
- Preferably have been used in previous, similar studies.
- Functionally important or be indicators of wider biodiversity.
- Preferably be well studied and have good taxonomic and ecological information available.

Birds, trees and dung beetles all meet these criteria to varying degrees. Some taxa will show idiosyncratic responses to land use change, however (e.g. Barlow et al., 2007) and so caution should be exercised when extrapolating from my results to other taxa.

## Birds

There is exceptional taxonomic and ecological information available on birds; they are relatively easy to survey; are found in all of Yucatán's terrestrial habitats; and show a range of responses to agriculture and habitat clearance. The region retains forest dependent species, as well as open habitat specialists and endemics that rely on the tropical dry forest and cactus shrub in the north of the peninsula (Howell and Webb, 1995). Importantly, much of the work on land sharing and sparing has examined birds' responses to agricultural yields (Phalan, 2009; Hulme et al., 2013; Kamp et al., 2015; Dotta et al., 2015; Feniuk, 2016). I therefore had the opportunity to add to a growing body of knowledge and to compare my results with studies in other regions and very different farming systems.

A lower proportion of birds are threatened than any other vertebrate taxon (IUCN, 2015), implying they are relatively robust to anthropogenic threats, although agriculture and the land use change it drives threatens more bird species than anything else (Green et al., 2005). In addition, several studies have found that birds good indicators for ecological and biological change (Barlow et al., 2007; Gardner et al., 2008) and that they are one of the most cost effective taxa to survey (Gardner et al., 2008). Birds are also charismatic and the declines of New World warblers (Parulidae) and other migratory species has driven a lot of the research into agriculturally driven biodiversity loss in Mexico (e.g. Rappole and McDonald, 1994), potentially giving my research greater political weight.

### Trees

Previous work on land sparing and land sharing has also studied trees (Phalan et al., 2011b; Feniuk, 2016), and although a large proportion of trees have not been assessed by the IUCN (IUCN, 2015), they are relatively well-studied, and readily surveyed and identified in the field (although in tropical forests this requires considerable knowledge and experience). Trees are also extremely functionally important: such is their importance to other taxa that they have been used to estimate the total number of species in the world (Erwin, 1982; Ødegaard, 2000). They also generate many ecosystem services including soil stabilisation, water flow and quality regulation and carbon sequestration and storage (e.g. Balmford et al., 2002; Daily et al., 2009). Finally, trees have huge cultural and religious importance and the ceiba (kaypok) *Ceiba pendrandra* is a fundamental part of Mayan mythology and hugely symbolic of the Maya even today (Zidar and Elisens, 2009).

### Dung beetles

True dung beetles of the subfamily Scarabaeinae are good indicators for ecological change (Barlow et al., 2007; Gardner et al., 2007) as they are found across agricultural and undisturbed habitats in the Neotropics (Estrada et al., 1998; Navarrete and Halffter, 2008; Nichols and Gardner, 2011), with some species showing strong responses to habitat disturbance (Estrada et al., 1998; Nichols et al., 2007; Nichols and Gardner, 2011). They are well documented in the Neotropics, more easily identified to species level than many insect taxa and are cost effective to sample through well defined survey protocols (Gardner et al., 2008). They also provide ecosystem functions such as burying dung, aerating soil, dispersing seeds and reducing parasitism rates in other species (Nichols et al., 2008). Several of these functions have been linked with valuable ecosystem services in cattle pastures (Giraldo et al., 2010). Unfortunately, only 577 species of Scarabaeidae (to which true dung beetles belong) have been assessed by the IUCN, of which 231 were data deficient (IUCN, 2015), although there are perhaps 5,000 members of Scarabaeinae alone.

### Previous studies in the YP

Several studies have investigated the recovery of bird and plant communities in the YP after natural and anthropogenic disturbances (Lynch, 1995; Smith et al., 2001; Lawrence and Foster, 2002; Boose et al., 2003; Read and Lawrence, 2003; Whigham

et al., 2003; Urquiza-Haas et al., 2007; Eaton and Lawrence, 2009; Bonilla-Moheno, 2012). However, I could not find any studies of variation between cattle pastures and natural habitats, although Cepeda-González et al. (2011) found that bird communities differed between pastures surrounded by anthropogenic and natural habitats. I could find no studies looking at tree biodiversity in cattle ranches in Yucatán.

Dung beetles are very poorly studied in the YP, although three studies have investigated dung beetle diversity in cattle ranches. Reyes Novelo et al. (2007) found diversity and species richness were highest in secondary vegetation and a *ramon* (breadnut) *Brosimum alicastrum* plantation respectively, compared to a cattle pasture, but the pasture had the highest abundance of individuals. Basto-Estrella and Rodríguez-Vivas (2012) and Basto-Estrella et al. (2013) investigated dung beetle communities across different cattle ranches and found that species richness, evenness and diversity were lower in ranches that used macrocyclic lactones (ML): antihelmithic drugs frequently used to treat cattle, but overall abundance of beetles was highest in the ranches that used MLs.

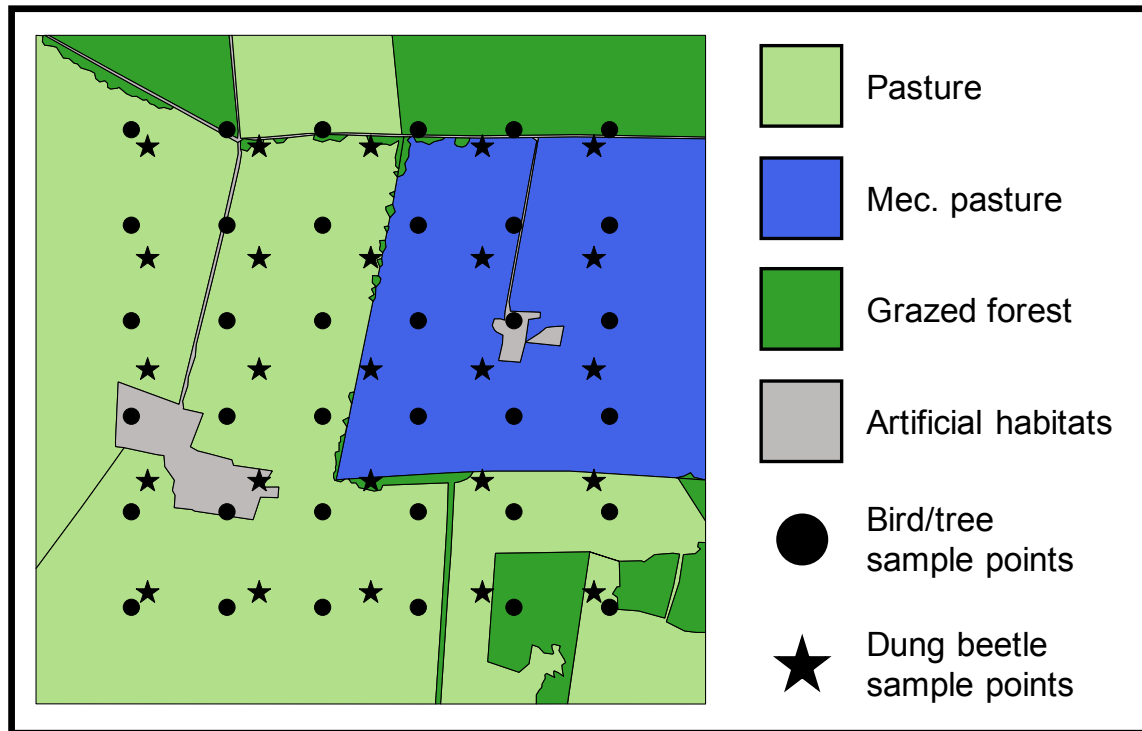
### 2.3.2 Methods

#### Data collection: Birds

Using QGIS I distributed 36 evenly spaced points across each study site, inset by 142 m to minimise edge effects (Fig. 2.4). I selected a subset of 24 of these without replacement, repeating the selection until the proportion of different land uses in the 70 m surrounding each point approximately matched their coverage in the site as a whole. In one *tecnificado* site the points could not adequately sample a patch of secondary regrowth so I moved five points to provide better coverage of this habitat, whilst keeping them entirely within the site.

The optimal time for surveying resident birds is during the breeding season, which is from April to July for most species (Howell and Webb, 1995). To ensure that I surveyed both early- and late-breeders, and to account for intra- and inter-annual variation, I visited most sites a total of four times (across three years): twice early in the breeding season (April-May) and twice later (late May-July). Due to problems with access and obtaining permission for two sites I was not able to visit them in 2012, and instead visited them twice in 2013 and twice in 2014. In one maize site I was refused permission to visit in 2014 and so only surveyed it on three occasions.

To survey birds I used point counts with distance sampling. Point counts are more efficient than mist netting (Whitman et al., 1997) and whilst line transects are



**Fig. 2.4** Map of an example study site showing sampling points for birds and trees (circles) and dung beetles (stars). I surveyed a subset of points for birds and trees. Dung beetles were sampled at all 25 points.

preferable in terms of analysis and sampling efficiency (Buckland et al., 2005), they were not practical due to the difficulty of moving through very dense vegetation, across multiple land holdings, or through fences and hedges.

To minimise disturbance I cut trails to each point, usually assisted by local *campesinos*, at least a day before the survey. At each point I surveyed birds for ten minutes in each point, without a settling-in period, identifying individuals to species and recording their distance from me. I completed all counts between half an hour before, and three hours after sunrise (following Blake, 1992). I counted dense groups as a single sighting, recording group size and measuring the distance to the centre of the group. Where possible I checked distances using a laser rangefinder, but it was normally impossible to judge exactly where birds were: 70% of detections were aural and the rangefinder did not work well in dense vegetation. To avoid inaccurate distance estimates I only recorded birds within 80 m of the point and subsequently discarded detections over 70 m away to avoid subconsciously including species ‘just within’ the 80 m. I recorded flying individuals for a single “snapshot” count at the end of each count.

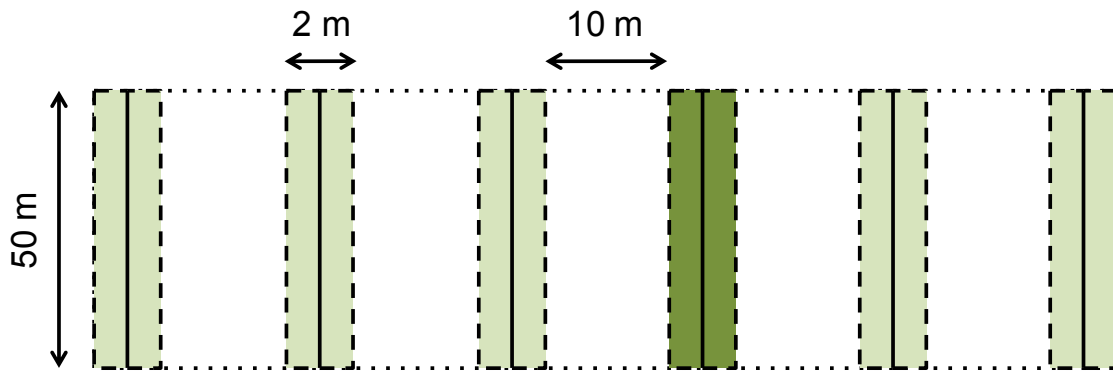
For all the surveys in 2012 and those in well-forested sites in 2013 and 2014 I was accompanied by one of four local experts (Paul Wood, Victor Marin Perez, Don Ramiro and Edilberto Poot). After each point we checked our independent records for the point to ensure that we were recording similar species, however this was done purely as a check and I did not alter my records based on what the experts saw and heard. I recorded each count using a Sony PCM-M10 digital recorder and a Sennheiser ME 66 shotgun microphone to check uncertain identifications.

### **Data collection: Trees**

To survey trees I visited a random subset of the 24 points surveyed for birds: 10 in baseline sites and one traditional ranch site that was entirely grazed forest, and 20 in other sites in order to increase the number of trees recorded and the reliability of population density estimates. I randomly picked points without replacement, repeating the procedure until the proportion in each habitat type matched the coverage of the habitats in the site as a whole. I designed the survey protocol, but trees were identified by two local experts: Don Miguel Poot (in one baseline site) and Edilberto Poot (all other sites). Either myself or my field assistant Tim Kasoar measured tree diameter at breast height (dbh), and myself plus at least one of Tim and the experts estimated tree heights.

In each point I used a modified Gentry plot (based on Baraloto et al., 2012, Fig. 2.5): six 2 m x 50 m transects running north-south and separated by 10 m. I surveyed all trees with a dbh of 10 cm or more in each transect and randomly chose one of the two central transects as a subplot in which I surveyed all trees with a dbh of 5 cm or more. The Gentry plot design was quicker to survey in dense vegetation than a 25 x 25 m plot whilst covering a larger area and better accounting for fine-scale heterogeneity in landscapes – important in Yucatán as soils and vegetation can vary over short distances (CONABIO, 2015). I included trees if the centre of the base of the trunk was within 1 m of the centre of the transect, flipping a coin if the centre appeared to be exactly 1 m away. I measured native and non-native tree species, including palms, but not lianas or herbaceous vegetation because of identification difficulties.

In each transect we identified and measured all stems above the threshold size, noting if they were from the same individual. Trees were identified by Mayan or Spanish name by the local experts. Most identifications were done on the basis of bark and leaves, with smell of crushed leaves and cut bark also being used by the guides. We measured dbh (following MacDicken, 1998) and estimated heights of trees by eye. Initially I used a clinometer but this greatly increased the time taken in forest



**Fig. 2.5** Modified Gentry plot used to survey trees. Solid lines indicate 50 m long transects, with shaded areas showing the area surveyed for trees with a dbh  $\geq 10$  cm. The darker shaded transect is the subplot where trees with a dbh  $\geq 5$  cm were sampled. Whether the third or fourth transect was used as the subplot was decided with the flip of a coin.

sites and seemed very unreliable due to difficulties in seeing the tops of trees in dense vegetation. At least two people out of me, my field assistant Tim Kasoar and my guide independently estimated heights and I recorded the range given if estimates differed.

#### Data collection: Dung beetles

Fredy and I designed the dung beetle survey protocol, but all data collection was by Fredy, his field assistants, and the team at INECOL.

To sample dung beetles we placed 25 regularly spaced traps across each site (Fig 2.4), far enough apart to reduce interference between traps (Larsen and Forsyth, 2005). Each trap consisted of a 1 l container with an 11.5 cm diameter opening buried to be flush with the ground and one quarter filled with a solution of water, salt and soap to prevent the beetles from escaping. Following Marsh et al. (2013) each trap was baited with approximately 20 g of a 1:1 mix of human and pig dung suspended over the trap. Traps were left for 48 hours and beetles placed in 70% alcohol solution before being identified to species by Fredy Alvarado and Fernando Escobar at INECOL, where voucher specimens were deposited. One maize site refused permission for dung beetle sampling, so we only have data from 24 sites.

#### Data processing: Birds

I discarded all records I could not identify to species, unless it was possible to place a bird in a group, such as “hummingbirds” or “kingbirds” (Couch’s and tropical kingbirds

*Tyrannus couchii* and *T. melancholicus* cannot be not reliably separated by sight, Traylor, 1979). In these cases I kept the records to fit detection functions (see below) but not to calculate species densities.

I discarded records of species that my techniques would not adequately sample: raptors, falcons and New World vultures (Accipitridae, Falconidae and Cathartidae); swallows and martins (Hirundinidae); swifts (Apodidae); and water birds (American purple gallinule *Porphyrio martinicus*, northern jacana *Jacana spinosa* and cattle egret *Bubulcus ibis*). I did, however, retain records of black-bellied whistling ducks *Dendrocygna autumnalis* because they frequently use harvested crop fields in sites far from standing water (*pers. obs.*). I discarded non-breeding migratory species because my field seasons did not coincide with peak migration times. For each retained species in each point I summed the total number of clusters observed and I also calculated the mean cluster size for each species across all sites.

### Distance sampling

I used distance sampling to account for the fact that habitat complexity affects how easily birds are detected, thereby altering the area effectively surveyed. I used the packages `{raster}` (Hijmans, 2015) and `{rgdal}` (Bivand et al., 2015) in R (version 3.1.1, R Core Team, 2015) to estimate the proportion of "closed" habitats (e.g. forests, hedges, secondary vegetation and high crops which reduced detectability) around each survey point and fitted detection functions using the package `mrds` (Laake et al., 2015). For 51 species with at least 30 observations, I fitted species-specific detection functions using the proportion of closed habitats as a continuous covariate; half-normal or hazard-rate key functions; and cosine, hermite polynomial and simple polynomial adjustment terms. I also grouped the majority of species into 23 detectability groups based on taxonomic, dietary and behavioural characteristics. I fitted detection functions to these groups including both the proportion of closed habitats and species as covariates, and using half-normal and hazard-rate key functions. I did not include nine species with more than 30 observations in these detectability groups because I did not consider that their detection functions were similar enough to those of other species.

I examined fitted models for goodness of fit using Chi-square, Kolmogorov-Smirnov and Cramer-von-Mises tests, as well as visually checking quantile-quantile plots and the shape of the detection function. For some species, all models either failed to converge or were rejected on one of the above criteria. In these cases, I used results from the multi-species models that included these species; in all other cases, I chose individual species models over multi-species models. Some multi-species models failed to converge



due to very low numbers of observations for certain species, so I grouped the species that were most similar to fit the detection function but performed subsequent analyses on individual species. Finally, for some species and groups (e.g. thicket tinamou *Crypturellus cinnamomeus*), detectability did not fall within 70 m so I assumed an effective detection radius of 70 m for every point.

Once I had a complete list of feasible detection functions I used AICc weightings and model averaging as described by Burnham and Anderson (2002) to get weighted detection functions.

### Data processing: Trees

I translated Mayan names to binomial names using a range of resources (CICY Herbarium, 2014; UCR Herbarium, 2014) and checked names with a standardised list (Boyle et al., 2013). I could not find translations for 55 of 177 species, but my guides were confident that they represented different species so I retained the records. For an additional five species the given name could refer to several species. In these cases I assumed all records were of the same species.

For biodiversity analyses I retained all identified species, even if I could not translate the name to a binomial, and also those that were identified to genus level. I discarded trees that the guides could not identify or which were from introduced or domesticated species. I did, however, retain both these groups for carbon stock estimation (Section 2.4).

### Data processing: Dung beetles

Once dung beetles were identified and counted I excluded a single introduced species: *Digitonthophagus gazella*.

### Data processing: Surveyed areas

To fit density-yield functions (Chapter 4) and calculate species or carbon densities (Chapters 5 and 6) I needed to know the area I had surveyed for each species.

For birds, I used the weighted detection functions to estimates of the effective detection radius for each species in each point and from this calculated effective detection area. I summed these across sites to get the total area surveyed. For trees, I used the total area of all Gentry plots in a site: 0.6 ha for forest sites and 1.2 ha for non-forest sites. It is not known how far dung beetles travel to baited pitfall traps and

so I could not reliably calculate the area surveyed. Instead I used the number of intact traps in each site as a measure of survey effort (after accounting for traps destroyed by animals).

### Assessing survey effectiveness

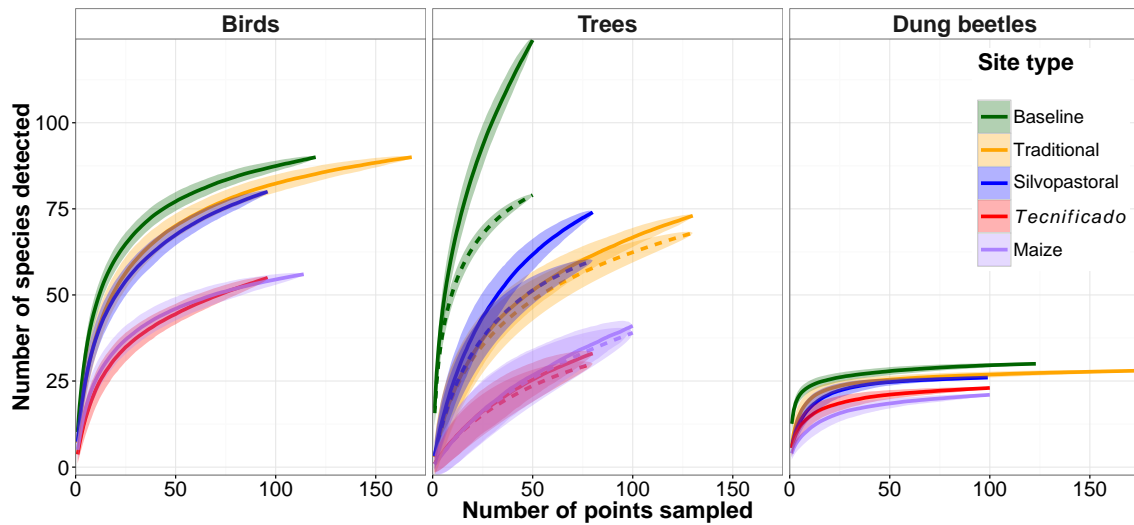
To assess my effectiveness at detecting all species present I plotted the expected mean species richness in each site type against the number of points surveyed. For this I used the function `specaccum` from the `{vegan}` package in R (Oksanen et al., 2015) and used Kindt’s exact method to estimate richness, as recommended by Oksanen (2013). I also used the function `specpool()` (also in `{vegan}`) to estimate species richness in each site using Chao1 and Jackknife estimators as recommended by Gotelli and Colwell (2001), with points as samples.

### 2.3.3 Results

After initial data processing, I was left with 6,626 records of 112 bird species and 5,336 trees of 154 species. Fourteen more trees were identified to one of four genera (*Malpighia*, *Spondias*, *Plumeria*, and *Cordia*) and two were described as “mora”, which could refer to the genus *Rubus* in Rosaceae or *Morus* in Moraceae. If I excluded trees that were not identified to species, or that I could not assign a binomial to, I was left with 5,197 trees of 100 species. I performed analyses on both datasets. One maize site had no trees recorded in it. We collected and identified 210,522 beetles of 32 species, a mean of over 175 beetles per trap-day: similar to the 162 found by Basto-Estrella and Rodríguez-Vivas (2012) and Basto-Estrella et al. (2013) in Yucatecan ranches, but considerably higher than other Neotropical studies (e.g. Horgan, 2007; Navarrete and Halffter, 2008).

### Survey effectiveness and species richness

Dung beetle accumulation curves nearly reached their asymptotes for all types of study sites (Fig. 2.6). Birds were slightly undersampled but had similar curve shapes across site types, so I consider that my results are unlikely to be biased. However I seriously undersampled trees, particularly in baseline sites, a pattern largely driven by rare species where the Mayan name could not be matched to a binomial name (Fig. 2.6). Because this undersampling was most severe in baseline sites my results will probably underestimate the biodiversity value of natural habitats, and possibly understate the potential benefits of land sparing.

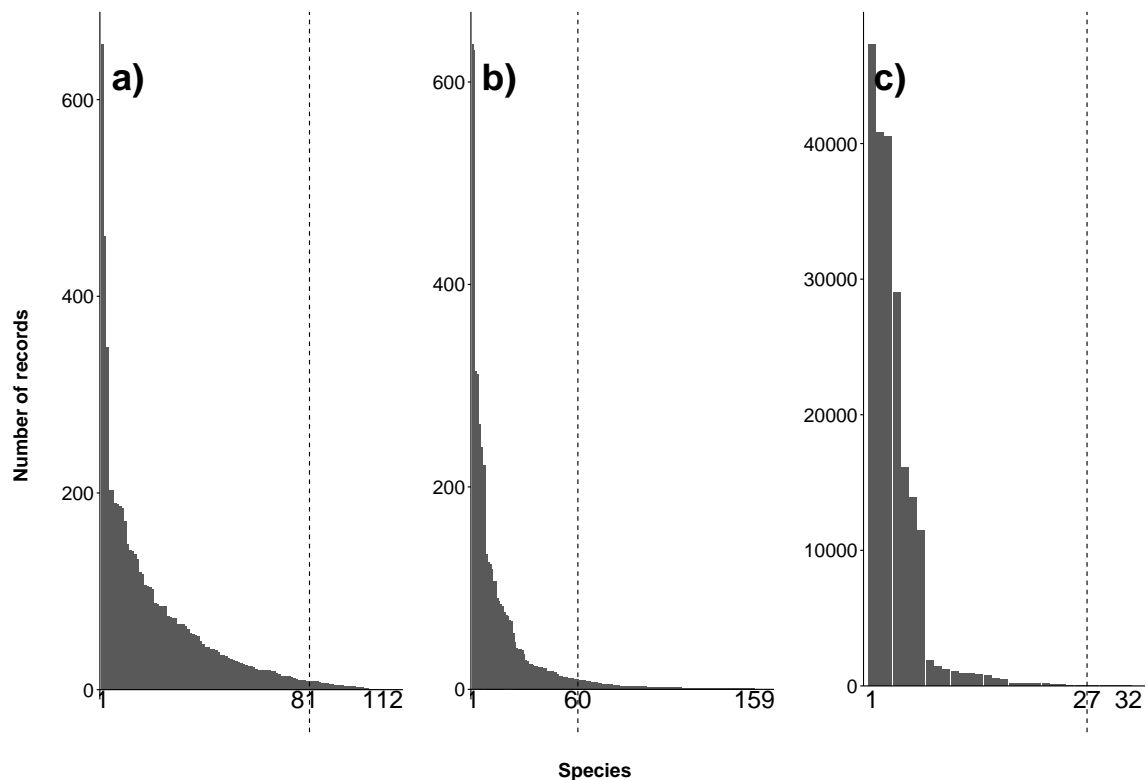


**Fig. 2.6** Species accumulation curves for different taxa in different study site types. Lines show mean number of species detected in 1,000 random samples taken without replacement. Shaded areas show the standard deviation around this mean. Dashed lines show accumulation curves for trees excluding species that could not be matched to a binomial name.

The highest values for observed and estimated species richness in individual sites were all in baseline sites, except for dung beetles where a traditional site had the same observed richness (25 species) as a baseline and a maize site had the highest Chao1 richness (Tables C.8–C.10). There was also a very high Chao1 estimate of 200 tree species for a maize site but this was based on 21 observed species. Observed and estimated species richness values were highest for baselines, except for birds, which had higher estimates in traditional sites (Fig. 2.6).

### Species present

A high proportion of tree species (99 of 159) had fewer than 10 records, compared to 32 of 112 bird species and five of 32 dung beetles (Fig. 2.7). One species of dung beetle (*Onthophagus landolti*) was found in all sites surveyed, with several birds and beetles only absent from two or three sites. Tree species were less ubiquitous, with only two species (*chaká* or gumbo-limbo *Bursera simaruba* and *guano* or savanna palm *Sabal mauritiiformis*) found in more than 20 sites.



**Fig. 2.7** Number of records for each species of **a)** birds **b)** trees and **c)** dung beetles. The dashed line separates species with more than and fewer than ten records. The numbers for trees include species without binomial names.

## 2.4 Carbon stock evaluation

### 2.4.1 Introduction

The relationship between carbon stocks and agriculture is extremely important because land clearance for agriculture is a major contributor to anthropogenic greenhouse gas emissions (Houghton et al., 2001; Foley et al., 2005). Conversely, combining high yield agriculture with forest protection or reforestation could sequester carbon and reduce net emissions (Lamb et al., 2016b).

Previous studies have examined carbon stocks in the YP (Lawrence and Foster, 2002; Cairns et al., 2003; Vargas et al., 2007; Eaton and Lawrence, 2009; Orihuela-Belmonte et al., 2013; Roa-Fuentes et al., 2013; Hernández-Stefanoni et al., 2014) but none have done so in cattle pastures, or linked their estimates to different land-use strategies. I estimated carbon stocks in my study sites using the live aboveground biomass, live

belowground biomass, soil carbon, and standing litter crop for each (MacDicken, 1998). Below I describe my methods for estimating each in turn.

## 2.4.2 Methods

### Aboveground biomass

To estimate aboveground biomass densities I used the same data as for my tree biodiversity surveys. For all trees except three species of palm I calculated the aboveground biomass of trees using Models (4) and (7) in Chave et al. (2014):

$$AGB_{est} = 0.0673(\rho D^2 H)^{0.976} \quad (4)$$

$$AGB_{est} = \exp(-1.803 - 0.976E + 0.976\ln(\rho) + 2.673\ln(D) - 0.0299\ln(D)^2) \quad (7)$$

where:

$AGB_{est}$  = estimated aboveground biomass of the tree (kg)

$\rho$  = species specific wood specific gravity ( $\text{g cm}^{-3}$ )

$D$  = diameter at breast height of the tree (cm)

$H$  = height of the tree (m)

$E$  = site-specific measure of environmental stress, comprising temperature seasonality, climatic water deficit and precipitation seasonality.

Model (4) performs better than Model (7) (Chave et al., 2014) and so I used it whenever I had height data, using the mean value when I had a range of height estimates. Otherwise I used Model (7), taking site-specific estimates of  $E$  from the 2.5 arc-second resolution raster layer produced by Chave et al. (2014) ([http://chave.ups-tlse.fr/pantropical\\_allometry.htm](http://chave.ups-tlse.fr/pantropical_allometry.htm)).

I obtained species specific wood density estimates from Zanne et al. (2009) and used mean estimates for genera where these were not available. I did not restrict my estimates to region-specific values because the only records for several species were from outside Central America. I used mean family values when genus-level estimates were not available and used the mean of all species in my database for trees that I could not match to a binomial name.

Palm biomass is not well described by allometric equations designed for dicotyledonous trees (Goodman et al., 2013) and so I used separate, family-level models described by Goodman et al. (2013):

$$AGB_{est} = -4.04054 + 2.34557\ln(D) + 0.76727\ln(H_{stem}) \quad (1)$$

$$AGB_{est} = \exp(-3.3488 + 2.7483\ln(D)) \quad (2)$$

where:

$AGB_{est}$  = estimated aboveground biomass of the palm (kg)

$D$  = diameter at breast height of the tree (cm)

$H_{stem}$  = height of the palm trunk i.e. excluding the crown (m)

Model (1) performs better than Model (2) and so I used it when I had height data. The performance of Model (2) falls considerably for palms with a dbh greater than 40 cm but I only recorded five palms (all *Acrocomia aculeata* from one site) with dbh values greater than 40 cm and no height recorded, so I judged that the error would not significantly alter my results.

I did not calculate biomass values for dead trees. If trees were partially dead then I scaled estimates by the proportion of the tree still alive.

I estimated site aboveground biomass densities by summing the biomasses of individual trees and dividing by the area surveyed. Because I surveyed different areas for small ( $5 < \text{dbh} < 10$  cm) and large ( $\text{dbh} \geq 10$  cm) trees I calculated densities separately for the two groups and then summed the two.

### Belowground biomass and total live carbon stocks

I used Equation (3), modified for tropical zones, from Cairns et al. (1997) to estimate root biomass density:

$$RBD_{est} = \exp(-1.0587 + 0.8836\ln(AGB_{est}))$$

where:

$RBD_{est}$  = estimated root biomass density ( $\text{Mg ha}^{-1}$ )

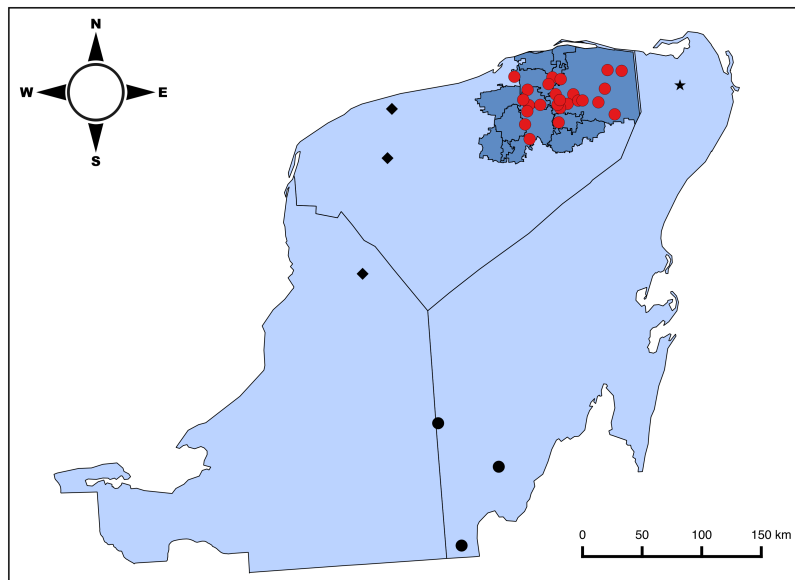
$ABD_{est}$  = estimated aboveground biomass density ( $\text{Mg ha}^{-1}$ )

I summed above- and belowground biomass density estimates for each site, converted these to carbon using the standard ratio of 0.5 (Brown and Lugo, 1982) and multiplied them by the area of each site (100 ha) to estimate total living carbon stocks.

To test whether I had effectively sampled my study sites, I performed a bootstrapping exercise: I randomly sampled with replacement from the points surveyed in each site and estimated aboveground carbon stocks for this sample before repeating the process 10,000 times. I calculated the mean and standard deviation of these estimates and saw how they changed with increasing sample size.

### Other carbon stocks and total carbon densities

Soil and standing litter crop can be important carbon stocks (e.g. Eaton and Lawrence, 2009) but logistical constraints prevented me from sampling them, so I used published values. I restricted my search to studies within the YP as it has extremely thin soils. I used Web of Science ([www.wok.mimas.ac.uk](http://www.wok.mimas.ac.uk)) and Google Scholar (<https://scholar.google.co.uk/>) to find three studies ranging across the climatic gradients and soil types in the peninsula (Fig. 2.8). I took mean values when studies had multiple study sites and summed all litter classes for each study.



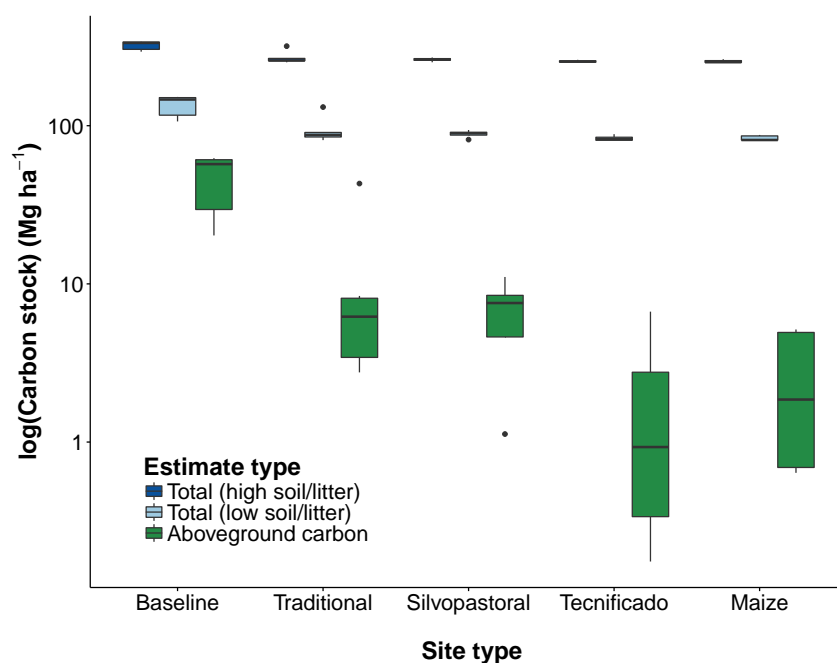
**Fig. 2.8** Location of studies used for soil and standing litter crop carbon stock estimation, relative to Tizimín District (dark blue area). Studies are: circles – Eaton and Lawrence (2009); squares – Roa-Fuentes et al. (2013); and star – Vargas et al. (2007). My study sites are shown as red circles.

I multiplied soil carbon densities by the area of each site, but judged that standing litter crop stocks would be close to zero in pastures and maize fields, so multiplied densities by the area of baseline habitat, grazed forest or secondary regrowth in a site.

I then summed the living carbon, soil carbon, and standing litter crop carbon stocks and divided by the area of each site to get a total carbon stock density.

### 2.4.3 Results

Excluding the maize site where no trees were recorded (see Section 2.3), aboveground carbon stocks ranged from 0.21 Mg ha<sup>-1</sup> in a *tecnificado* site to 67.9 Mg ha<sup>-1</sup> in a baseline site. Baseline sites had higher live (and therefore total) carbon stocks than all other sites except for the traditional ranch site entirely covered in grazed forest (Fig 2.9). Four of the baseline sites had aboveground stocks within the range of published values: from 47 Mg ha<sup>-1</sup> in north west Yucatán State (Roa-Fuentes et al., 2013) to 377 Mg ha<sup>-1</sup> in southern Quintana Roo (Hernández-Stefanoni et al., 2014). Lower values for the other baselines may reflect the fact that some published studies sampled trees down to 1 cm dbh, or the fact that my baseline sites were relatively young and aboveground carbon stocks increase with time after disturbance (Eaton and Lawrence, 2009).



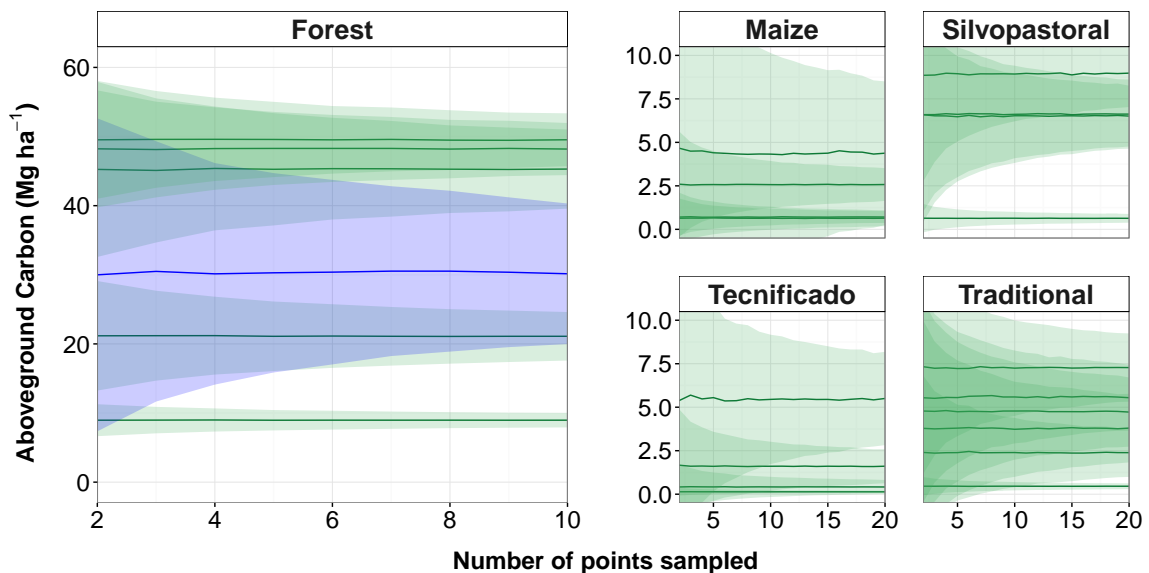
**Fig. 2.9** Total and aboveground carbon stock estimates in different types of study site using both high and low estimates for soil and standing litter crop estimates.



Published soil estimates ranged from 80 Mg ha<sup>-1</sup> in the El Eden reserve (50 km to the east of my study sites, Vargas et al., 2007) to 250 Mg ha<sup>-1</sup> in the Calakmul Biosphere Reserve (250–350 km to the south, Eaton and Lawrence, 2009), whilst standing litter crop stocks ranged from 3.8 Mg ha<sup>-1</sup> in north-west Yucatán (Roa-Fuentes et al., 2013) to 21 Mg ha<sup>-1</sup> in Calakmul. Given its proximity, I suspect soil carbon stocks in my study sites are closer to Vargas et al.'s estimates than Eaton and Lawrence's, but I used both the highest and lowest values to see what effect variation in soil carbon stocks would have on my conclusions.

Even with lower estimates, soil carbon contributed over 50% of stocks in all sites and over 99% in six productive sites. This seems surprising given the very thin soils in Yucatán but these values are similar to those obtained in other studies in mature forest in the YP: 54% of carbon stocks coming from soils in El Eden (Vargas et al., 2007) and 84% in Calakmul (Eaton and Lawrence, 2009).

The bootstrapping exercise revealed that estimated aboveground carbon stock estimates were consistent with increasing sample size, giving assurance that I had sampled sufficient points to reliably estimate aboveground carbon stocks (Fig. 2.10). There was considerable variation around each mean estimate, which may reflect the heterogeneous nature of my study sites.



**Fig. 2.10** Variation in aboveground carbon stock estimates with increasing sample size. Dark lines represent the mean value of 10,000 random samples, shaded areas the standard deviation (darker shaded areas show where multiple standard deviations overlap). Note the different y-axis scales, reflecting the far greater carbon stocks in forest sites. The non-baseline forest site is shown in blue on the left-hand graph.

## 2.5 Using these data

The methods outlined in this chapter provide:

- 25 study sites and the land uses within them.
- Interview data for 77 ranches, with information on land uses present, production of animals and fodder crops, and ranch requirements. I use these data in Chapter 3 to estimate the yields and requirements of different land uses and feed conversion ratios.
- Biodiversity data for each study site. Specifically, I have data on the number of clusters of birds and mean cluster size for each species; the number of trees and dung beetles; and species identity and sampling effort (either area surveyed or number of traps). I use these data to investigate how species' population densities respond to agricultural yields (Chapter 4) and how different land-use strategies are likely to affect regional population sizes (Chapter 5).
- Carbon stock estimates for each study site, which I use in Chapter 6 to investigate how carbon stocks vary with agricultural yield and land-use strategies.





## CHAPTER 3

### ESTIMATING YIELDS AND PRODUCTION IN LIVESTOCK SYSTEMS

---

*“The cow is nothing but a machine which makes grass fit for us people to eat”*

John McNulty

#### 3.1 Introduction

##### 3.1.1 Measuring agricultural impact

A range of indices can be used to measure agricultural practices: generalised measures of ‘agricultural intensity’ (Bignal and McCracken, 1996; Wade et al., 2010; Mastrangelo and Gavin, 2014), uptake rates of broad agricultural strategies such as agroforestry (Bhagwat et al., 2008; Garcia et al., 2010) or organic agriculture (Hole et al., 2005; Gabriel et al., 2010), or changes to specific practices such as fertiliser or pesticide use (Frampton and Dorne, 2007). However many of these measures fail to account for the impacts of agriculture across both farmland and natural habitats: if practices to increase on-farm biodiversity reduce yields then a larger area will be needed to meet food or economic demands, potentially leading to greater habitat conversion (Balmford et al., 2012). These externalised impacts can be accounted for by investigating agricultural yields (production per unit area) and by looking at how agricultural practices affect overall land-use patterns for region.

In this chapter I explain how I derived the key variables needed to estimate the yields, production and requirements of my study sites. First, I estimated the yields of individual sites based on only on the land uses present in them - from the yields of

different grazed land uses and of maize and fodder grass fields. I used these estimates to construct density-yield functions for individual species (Chapter 4) and carbon stocks (Chapter 6). Second, I estimated the the maize used by each site alongside the extra production this provides, and the calves required by finishing ranches. These data were then used to design scenarios for investigating how different land-use strategies affect regional populations of species (Chapter 5) and regional carbon stocks (Chapter 6).

## 3.2 Methods

To estimate a site's yields for constructing density-yield functions I combined the yields of individual land uses with land cover data for a site, and used conversion ratios to convert these values into a single currency. I then summed production across land uses and divided by the total area of the site to produce a yield. To build land-use scenarios I also estimated each site's maize and calf requirements, again converting these to a single currency.

I chose kilograms of finished cow protein per hectare as my currency because it is demand for meat (rather than food energy), that is driving agricultural expansion in Tizimín District (TD) and because I was not able to get enough high quality economic data to accurately model economic yields.

In addition to the area of each land use in each site, I therefore needed to estimate:

- Annual yields of maize and fodder grass ( $\text{t ha}^{-1} \text{ yr}^{-1}$ ).
- Grazing yields: the annual production, in kilograms of animal protein, attributable to animals grazing one hectare of a grazed land use ( $\text{kg animal protein ha}^{-1} \text{ yr}^{-1}$ ).
- Feed conversion ratio: the kilograms of animal protein produced for each tonne of maize used as feed.
- Calf conversion ratio: the kilograms of finished cow protein eventually produced for each kilogram of calf protein that enters a finishing ranch. The inverse is the calf requirement ratio: the kilograms of calf protein required for each kilogram of finished cow produced.
- Maize use: annual use of maize equivalents for each hectare of a grazed land use ( $\text{t ha}^{-1} \text{ yr}^{-1}$ ).

To estimate these variables I used the quantitative interview data described in Section 2.2. For each of the 77 ranches in my final data set I had the following data:

- Annual net production of animal protein ( $\text{kg yr}^{-1}$ ).

- Areas of each type of grazed land use (ha).
- Annual fodder use ( $\text{t yr}^{-1}$ ).
- Mean mass of animals entering and leaving the ranch (kg).
- Annual yields of maize and fodder grass ( $\text{t ha}^{-1} \text{ yr}^{-1}$ ).

I was able to estimate maize and fodder grass yields directly from interview and database data (Section 3.2.1), but needed to model the other variables. I derived grazing yields and feed conversion ratios using the Protein Production Model (Section 3.2.2); the calf conversion ratio using data on the mean mass of calves and finished cows (Section 3.2.3); and maize use using the Maize Use Model (Section 3.2.4). All the calculations and data required are summarised in Table 3.1.

**Table 3.1** Summary of the calculations I used to estimate yields in Yucatecan ranches. Estimates from calculations (2), (3) and (5) may vary between breeding and finishing ranches.

Variable	Data required	Solution
<b>(1) Maize and fodder grass yields</b> Tonnes of maize produced per hectare	Hectares of maize and fodder grass in ranches Production of maize and fodder grass by ranches Published yields	Calculate yields (Section 3.2.1)  Use published values
<b>(2) Grazing yields</b> Kilograms of animal protein produced per hectare of grazed land per year	Hectares of land uses in ranches Maize equivalents used by ranches Net protein production of ranches	Protein Production Model (Section 3.2.2)
<b>(3) Feed conversion ratio</b> Kilograms of animal protein produced per tonne of maize used	Hectares of land uses in ranches Maize equivalents used by ranches Protein production of ranches	Protein Production Model (Section 3.2.2)
<b>(4) Calf conversion ratio</b> Kilograms of calf protein required by a finishing ranch for each kilogram of finished cow produced	Mass of cows leaving ranches Mass of calves entering ranches	Calculate conversion ratio (Section 3.2.3)
<b>(5) Maize use</b> Tonnes of maize equivalents used annually by each hectare of grazed land	Hectares of land uses in ranches Maize equivalent use by ranches	Maize Use Model (Section 3.2.4)

### 3.2.1 Calculation (1): Maize and fodder grass yields

Few producers had information on maize and fodder grass yields, so I did not feel these would be reliable estimates. Instead I used a combination of the maximum reported yields (as an upper bound for my yield estimates) and yields recorded by the agricultural ministry (SAGARPA, 2015) as a lower bound. As described in Chapter 2, I used metabolisable energy to convert all values into tonnes of maize equivalents.



### 3.2.2 Calculations (2) and (3): Grazing yields and feed conversion ratio

To estimate grazing yields and the feed conversion ratio I parameterised what I termed the “Protein Production Model”:

$$P_i = \sum A_{ij}\alpha_j + M_i\beta$$

where:

$P_i$  = net annual production of ranch  $i$  (kg animal protein ha<sup>-1</sup> yr<sup>-1</sup>)

$A_{ij}$  = area of land use  $j$  in ranch  $i$  (ha)

$\alpha_j$  = grazing yield: annual kilograms of animal protein attributable to grazing one hectare of land use  $j$  (t ha<sup>-1</sup> yr<sup>-1</sup>)

$M_i$  = tonnes of maize equivalent used annually in ranch  $i$  (t yr<sup>-1</sup>)

$\beta$  = feed conversion ratio: the kilograms of animal protein produced by feeding animals one tonne of maize equivalent

I obtained estimates of  $\alpha$  and  $\beta$  by fitting a multiple linear regression of  $P$  on  $A_{ij}$   $M$ , without intercepts and with the coefficients constrained to be positive (given it is extremely unlikely that production will decline as the area of grazed land, or the amount of maize used increases). I fitted models using the `port` algorithm of the function `nls()` in R version 3.2 (R Core Team, 2015). `nls()` is an iterative procedure and sensitive to starting parameter estimates, so I first fitted unconstrained linear regressions without intercepts for the response variable ( $P$ ) against each explanatory variable ( $A_j$  and  $M$ ) in turn, and used the slopes of these regressions as my starting estimates.

To assess possible differences between breeding and finishing ranches I fitted models for all ranches combined, and to breeding and finishing ranches separately; using an F-test to compare the residual deviance of the combined model against the summed residual deviances of the two separate models. I also used F-tests to compare models that split or combined habitat types, specifically comparing:

- Splitting or combining grazed forest and younger secondary regrowth.
- Splitting or combining mechanised pasture and irrigated pasture.

### 3.2.3 Calculation (4): Calf conversion ratio

To estimate the kilograms of finished cow protein eventually produced for each kilogram of calf protein I used the ratio of masses of finished cows and calves:

$$Calf\ Conversion\ Ratio = \frac{Mass_{cow}}{Mass_{calf}}$$

The inverse of this is the calf requirement ratio: the kilograms of calf protein that each kilogram of finished cow protein requires.

### 3.2.4 Calculation (5): Maize use

To estimate the maize use per hectare of grazed land I used a similar method as for the Protein Production Model to parameterise what I termed the “Maize Use Model”:

$$M_i = \sum A_{ij} \lambda_j$$

where:

$M_i$  = tonnes of maize equivalent used annually in ranch  $i$  (t yr<sup>-1</sup>)

$A_{ij}$  = hectares of land use  $j$  in ranch  $i$  (ha)

$\lambda_j$  = estimated maize use: tonnes of maize used annually per hectare of land use  $j$  (t ha<sup>-1</sup> yr<sup>-1</sup>)

Again, I fitted a positively constrained multiple linear regression without an intercept to estimate  $\lambda_j$  using the `port` algorithm of `nls()`, and used linear regressions without intercepts to obtain starting values. I used F-tests to assess possible differences between breeding and finishing ranches; between grazed forest and younger regrowth; and between mechanised and irrigated pastures.

### 3.2.5 *Completo* ranches

*Completo* ranches are relatively rare in the region and I was not able to interview sufficient producers to parameterise separate Protein Yield and Maize Use Models for them. I therefore assumed that land in *completo* ranches was split evenly between breeding and finishing production. Protein yields and maize use would therefore be the mean of the values for breeding and finishing ranches.

### 3.2.6 Testing the sensitivity of my results

To test the robustness of my yield estimates, I performed a bootstrapping exercise. I took a random sample with replacement from the interview data and fitted the Protein Yield and Maize Use Models to it. I repeated the sampling 10,000 times and took the mean and standard deviation of the derived estimates. I then examined how the mean and standard deviation varied as I increased the sample size.

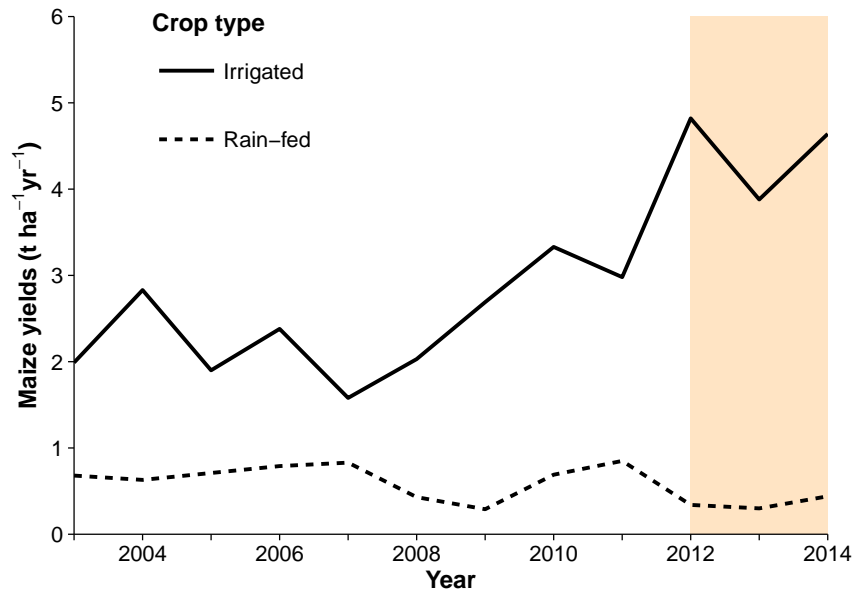
## 3.3 Results

### 3.3.1 Calculation (1): Maize and fodder grass yields

My study sites all reported higher maize and fodder grass yields than the mean yield for TD: 7–8 t ha<sup>-1</sup> for maize and 12.1 t ha<sup>-1</sup> for fodder grass (equivalent to 7.26 t ha<sup>-1</sup> of maize equivalents), compared with 3.02 t ha<sup>-1</sup> and 7.62 t ha<sup>-1</sup> for TD for the period 2003–2014 (SAGARPA, 2015). This is possibly because my maize sites were large, specialised ranches, whereas many producers only have a small area of maize without the infrastructure needed to raise yields. I therefore decided to use the maximum reported yields as an upper bound, and the regional maize yield (3.02 t ha<sup>-1</sup>) as a lower bound. Bounding my estimates in this way means that I can test the sensitivity of my results to a wide range of potential yields, and also allows for the possibility that my fieldwork years were unusually high yielding (Fig. 3.1). I used regional yields of irrigated, but not rainfed maize, as the vast majority of maize grown for cattle in TD is irrigated (*pers. obs.*), whilst rain-fed maize is largely part of traditional *milpa* agricultural systems and has lower yields (Fig. 3.1).

### 3.3.2 Calculations (2) and (3): Grazing yields and feed conversion ratio

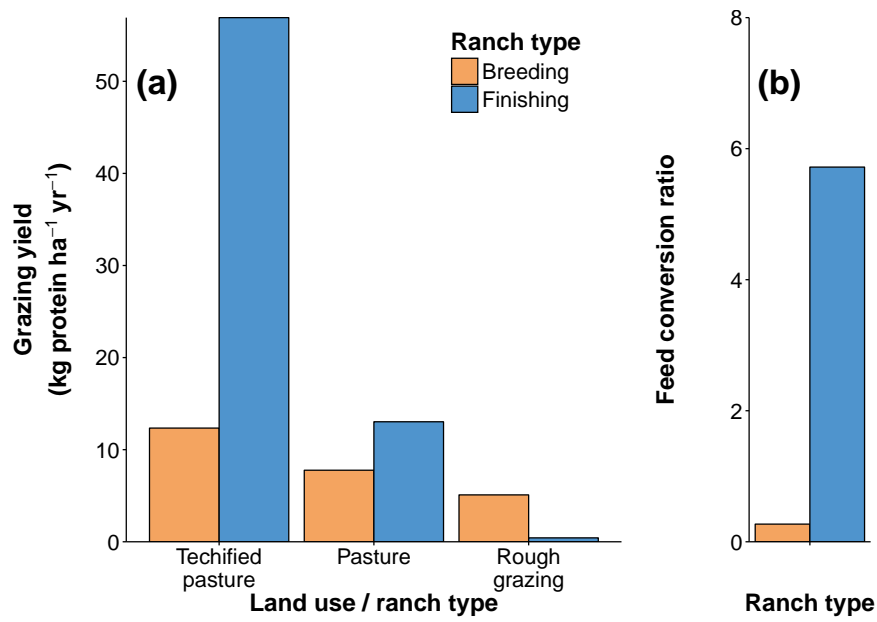
There was strong support for splitting breeding and finishing ranches in the Protein Production Model ( $F_{4,69} = 14.4$ ,  $p < 0.0001$ ), but not for splitting mechanised pasture from irrigated pasture, or grazed forest from younger secondary regrowth (Table 3.2). I therefore combined these land uses for subsequent analyses and refer to them as “technified pasture” and “rough grazing”, respectively. Grazing yields in both breeding and finishing ranches were highest for mechanised pasture followed by pasture and then grazed forest (Fig 3.2, Table 3.3). Finishing ranches had higher grazing yields for all land uses except rough grazing, and a higher feed conversion ratio.



**Fig. 3.1** Mean reported yields for irrigated and rain-fed maize in TD for 2003–2014. Data obtained from (SAGARPA, 2015). Shaded region indicates my fieldwork years.

**Table 3.2** Model comparisons for Protein Production and Maize Use Models.

Model	Production	Comparison	F-test	p-value
Protein Production Model	Breeding	Grazed forest vs. regrowth	$F_{1,44} = 2.73$	0.106
		Irrigated vs. mechanised pastures	$F_{1,44} = 2.32$	0.135
	Finishing	Grazed forest vs. regrowth	$F_{1,23} = 0.005$	0.944
		Irrigated vs. mechanised pastures	$F_{1,23} = 0.907$	0.351
Maize Use Model	Breeding	Grazed forest vs. regrowth	$F_{1,45} = 0.044$	0.835
		Irrigated vs. mechanised pastures	$F_{1,45} = 2.86$	0.100
	Finishing	Grazed forest vs. regrowth	$F_{1,24} < 0.001$	1.000
		Irrigated vs. mechanised pastures	$F_{1,24} = 0.046$	0.832



**Fig. 3.2** Grazing yield (a) and feed conversion ratio (b) estimates from the Protein Production Model.

### 3.3.3 Calculation (4): Calf conversion ratio

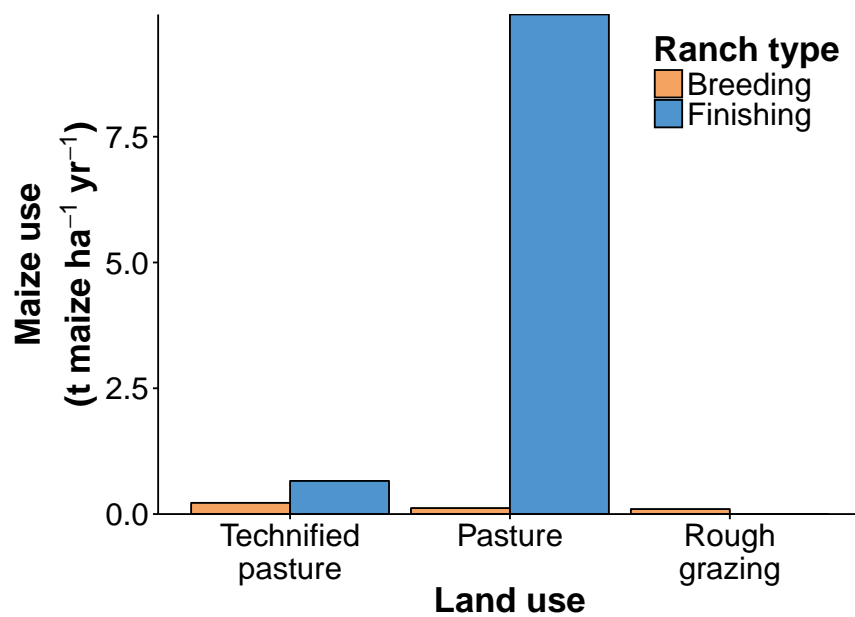
The modal mass for animals leaving ranches was 200 kg for breeding ranches, and 500 kg for finishing ranches. I therefore estimated the calf conversion ratio as:

$$\text{Calf Conversion Ratio} = \frac{500}{200}$$

This means that one kilogram of calf protein is on average converted into 2.5 kilograms of finished cow protein. The calf requirement ratio is the inverse of this, meaning that finishing ranches require 0.4 kilograms of calf protein to be supplied for each kilogram of finished cow protein that they produce.

### 3.3.4 Calculation (5): Maize use

There was strong support for splitting breeding and finishing ranches in the Maize Use Model ( $F_{3,71} = 118$ ,  $p < 0.0001$ ) but no support for splitting mechanised pasture from irrigated pasture or grazed forest from younger secondary regrowth (Table 3.2). Maize use was higher in finishing ranches for pasture and technified pasture, with pasture in finishing ranches having by far the highest use rates. Maize use was lowest in rough grazing, which was the only land use with higher use rates in breeding than finishing ranches (Fig. 3.3, Table 3.3).



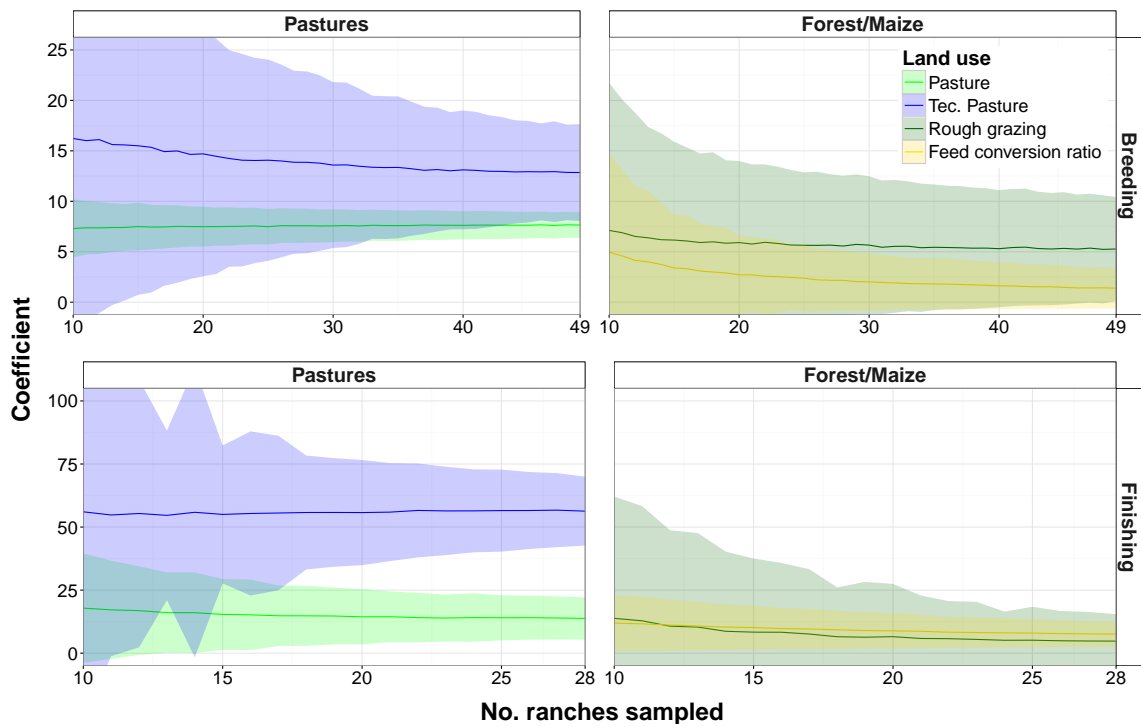
**Fig. 3.3** Tonnes of maize used per hectare of grazed land uses in breeding and finishing ranches.

**Table 3.3** Yields and maize use rates for grazed land uses in breeding and finishing ranches.

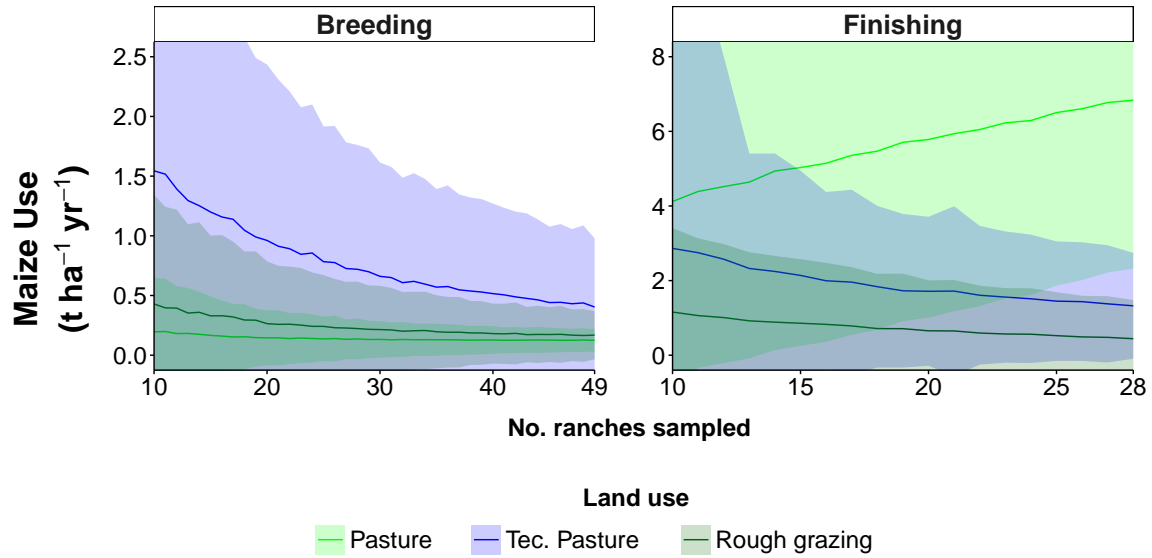
Production Type	Land Use	Grazing Yield (kg ha <sup>-1</sup> )	Maize Use (t ha <sup>-1</sup> )
Breeding	Technified pasture	12.3	0.222
	Pasture	7.77	0.119
	Rough grazing	5.09	0.0996
Finishing	Technified pasture	56.9	0.658
	Pasture	13.0	9.93
	Rough grazing	0.425	0.00

### 3.3.5 Sensitivity of these results

Bootstrapping demonstrated considerable variation in protein production (Fig. 3.4) and maize use (Fig. 3.5) estimates, but the mean of estimates remained relatively constant as the number of ranches sampled increased, giving me confidence that larger sample sizes would result in similar estimates. The exception is maize use in pasture in finishing ranches, which steadily increased. I therefore performed further sensitivity analyses when investigating the biodiversity and ecosystem service impacts of different land-use strategies (Sections 4.2.4, 5.3.2, 5.5.3).



**Fig. 3.4** Results of the bootstrapping exercise showing how the mean and standard deviation of estimates from the Protein Production Model varied as sample size increased. Dark lines show the mean of the 10,000 samples taken, shaded areas show the standard deviations. Coefficient values are in kg protein ha<sup>-1</sup>yr<sup>-1</sup> (grazed land uses) and t<sup>-1</sup> yr<sup>-1</sup> (feed conversion ratio).



**Fig. 3.5** Results of the bootstrapping exercise showing how the mean and standard deviation of estimates from the Maize Use Model varied as sample size increased. Dark lines show the mean of the 10,000 samples taken, shaded areas show the standard deviations.

## 3.4 Discussion

### 3.4.1 Differences between breeding and finishing ranches

The significant differences between breeding and finishing ranches for the Protein Production and Maize Use Models arise from their different management regimes and energetic needs. Breeding ranches maintain a breeding herd of animals that are not fattened for slaughter. These animals do not contribute to production as I measured it but consume a large proportion of the energy available from grazing or fodder inputs (Pelletier et al., 2010) leading to lower estimates for grazing yields and feed conversion ratios in the Protein Production Model. Breeding animals will be fed just enough fodder to maintain condition and ensure that they can produce calves, whereas those in finishing ranches may be fed large amounts of fodder to maximise weight gain – hence the lower estimates for breeding ranches from the Maize Use Model. Calves in breeding ranches will be fed large amounts of fodder, but as smaller animals their rates of consumption will be relatively low.

Rough grazing differs from this pattern, with higher maize use and grazing yields in breeding than finishing ranches. Rough grazing is used to maintain animals during the dry season, rather than to fatten them, and is more commonly used in breeding than



finishing ranches, which are more likely to increase fodder inputs to survive the dry season (*pers. obs.*). Breeding ranch producers may therefore take the area of rough grazing into account when estimating the herd they can maintain, meaning it will influence the production and maize use of a ranch. Producers in finishing ranches, however, are likely to ignore rough grazing when judging their herd size, meaning it will have little effect on either production or maize use.

### 3.4.2 Patterns in yields and maize use between land uses

Technified pasture had the highest grazing yields due to higher quality soils than pasture and correspondingly greater grass growth. These improved soils may also explain the lack of difference between mechanised and irrigated pastures, if deeper soils are more important in determining yields than is irrigation. This idea is supported by the observation that mechanised pastures maintained far better forage late in the dry season than non-mechanised pastures. Ranches with large areas of either mechanised or irrigated pasture tend to have similar animal management regimes (with rotational grazing, and high rates of antihelminthic use) and this probably explains the lack of difference between maize use for irrigated and mechanised pastures. Alternatively, because only seven of the 77 ranches I used to fit the models had mechanised, but non-irrigated, pastures, my models may have lacked sufficient power to distinguish between land uses.

The low grazing yields for rough grazing probably reflect the fact that these areas are rarely actively managed. Few producers plant or promote nutritious plants such as *Brosimum alicastrum* or *Leucaena leucocephala*, and instead use grazed forest to provide shade and relatively low quality fodder during the dry season. This ‘safety net’ role may also explain their low maize use, as they act in effect as a substitute for maize during the dry season. In contrast, pastures had very high maize use rates, which were needed to maintain animals when grass growth fell due to a lack of water and poor soils. Finally, from conversations with producers it was apparent that they viewed grazed forests and secondary regrowth similarly, so producers will not vary their management based on which of the two is present. This may reflect the fact that the forage or shade provided will not vary much with vegetation age, which would also explain why grazing yields did not differ. Another possibility, however, is that producers varied in their definitions of different vegetation types. I could not visit every patch of forest/regrowth described, and so relied on producers’ classifications. If these varied, then differences between land uses could be obscured.

### 3.4.3 Appropriateness of different yield metrics

Agricultural production is comprised of multiple currencies that need to be converted to a single metric to allow comparisons across sites and systems. Using simple nutritional metrics such as energetic or protein yields will lose details of exactly which nutrients are provided (e.g. DeFries et al., 2015), but can be used to explore how to meet specific production targets based on a population's demands. Economic yields cannot be used to set production targets in this way because economic gains can be substituted by other income sources in a way that food cannot. Economic yields can, however, include inputs, such as labour, and allow comparisons between very different products, for example staples, such as rice, and cash crops, such as cocoa or bananas.

I chose to use kilograms of finished cow protein produced per hectare as my metric, because it is demand for meat specifically that is driving agricultural expansion in TD and because I was not able to get enough high quality economic data to accurately model economic yields. In particular, producers were unable or unwilling to provide information on the capital costs of clearing forest for pasture (a process which pre-dated most of the producers I interviewed) or the costs of harvesting maize.

In reality, neither nutritional nor economic yields are likely to completely capture the proximate drivers to which producers respond. Farmers will probably seek to do more than simply maximise profits per hectare: capital costs; crop reliability and resilience; personal expertise; and social context are all likely to influence their decisions. Understanding the drivers of farmer behaviour is extremely important for conservation (e.g. Angelsen, 2010; Ceddia et al., 2014) but the detailed social and economic research needed to investigate them is beyond the scope of my thesis. Instead, my analyses focus on identifying the land-use strategies that can balance food production and biodiversity conservation, not the factors that influence farmer behaviour.

### 3.4.4 Potential issues with models

Standardising land uses and fodder types into a small number of categories could potentially reduce the accuracy or reliability of my yield estimates: land uses can vary with the forage species present or management intensity, and whilst energy is the most frequently limiting factor in Yucatecan ranches (Baba, 2007), fodders provide many other nutrients, meaning that producers could import equal quantities of fodder in terms of metabolisable energy, but gain very different yields, depending on their knowledge of their animals' requirements. Finally, ranches may vary in management regime and husbandry. High intensity rotational grazing, for example, has been promoted by

some as a higher-yielding method of animal management (e.g. Norton 1998 but see Briske et al. 2007); whilst anthelmintic drugs (Sutherland and Leathwick, 2011) and supplements (Moore et al., 1999) can also affect production.

### 3.4.5 Conclusions and how to use these estimates

I found that technified pastures had the highest grazing yields for both breeding and finishing ranches, followed by pasture and then rough grazing. Grazing yields and feed conversion ratios were higher for finishing than breeding ranches, as were maize use rates, except for in rough grazing. I also estimated maize and fodder grass yields and both calf conversion and calf requirement ratios.

In the following chapters I used these estimates in two ways. To describe the yields of my study sites for density yield functions I used the maize and fodder grass yields and grazing yields, combined with the land uses in each site to calculate the production of maize, calves and cows. I then used the feed conversion ratio for finishing ranches and the calf conversion ratio to convert all production values to finished cow equivalents. I then used this value to construct density yield functions for species (Chapter 4) and carbon stocks (Chapter 6).

To estimate the production and requirements of alternative region-wide land-use scenarios I calculated the production of each site as above. However, I also estimated the maize use of the sites and used the feed conversion ratios to calculate the extra production that this would result in. In finishing ranches I also used the calf conversion ratio to calculate the calves required. I then used these figures for maize production and use, calf production and requirements, and finished cow production to construct scenarios to investigate the impacts of different land-use strategies on species' regional populations (Chapter 5) and regional carbon stocks (Chapter 6).



## CHAPTER 4

### SPECIES' RESPONSES TO YIELDS

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*“Everyone likes birds. What wild creature is more accessible to our eyes and ears, as close to us and everyone in the world, as universal as a bird?”*

David Attenborough

#### 4.1 Introduction

In this chapter I will explore the effects of increasing agricultural yield on the population densities of birds, trees and dung beetles in Yucatecan cattle ranching landscapes. I start by explaining why I chose to investigate population density as my biodiversity metric, and the uses and limitations of density-yield functions in my study system. I then describe how I fitted density-yield functions and identified the land-use strategies that allow the highest population density of each species to survive for any given target yield. Finally I investigate variables that can help explain how species respond to agriculture.

##### 4.1.1 Biodiversity and yield metrics

Species richness and diversity indices are commonly used to investigate the impacts of agricultural practices on biodiversity (e.g. Perfecto et al., 2005; Steffan-Dewenter et al., 2007; Bhagwat et al., 2008; Clough et al., 2011) but fail to take into account either species identity, or variation in population size and hence the probability of species persistence in a landscape.

Species identity is important because not all species are equal from a conservation perspective: species with restricted habitat specificity, small range sizes and small local population sizes are likely to be of greater conservation concern than adaptable, wide ranging species with large local populations (Rabinowitz et al., 1986). Species richness does not capture the probability of persistence as it is based on presence-absence data, and a species' presence in a landscape does not guarantee that it has a healthy population there. Information on population density is far better, because larger populations are more likely to survive in the long-term (e.g. Berger, 1990). It does not include information on migration, reproductive rates or survival and so cannot identify if populations are viable, but these detailed demographic data are unfeasible to collect for hundreds of species across dozens of study landscapes. Steps can also be taken to ensure that population density is more likely to reflect probability of persistence: using buffer zones reduces edge effects, whilst studying landscapes that have not been recently altered can help allow for relaxation time (Diamond, 1972; Tilman et al., 1994; Brooks et al., 1999), although extinction debts may last for many years (Tilman et al., 1994; Brooks et al., 1999).

#### **4.1.2 Uses and limitations of density-yield functions**

Density-yield functions can be used to describe how species population densities respond to increasing agricultural yields (Green et al., 2005). This provides valuable information on the ecological or evolutionary traits that may influence how species respond, and so allow the development of models to predict the least damaging land-use strategies without having to collect data on individual species. Previous studies have also used density-yield functions to investigate how different ways of producing food are likely to affect regional species populations (e.g Phalan et al., 2011b; Hulme et al., 2013; Dotta et al., 2015; Kamp et al., 2015). This makes sense if individual study sites can be approximated to a self-contained system, because the land uses in any one site could be scaled up to meet an overall production target (although in reality, most study sites require external inputs such as fertilizers or food for workers). Yucatecan cattle ranches, however, are much further from being self-contained. My study sites produce (in varying proportions) three interdependent currencies: finished cows, calves and maize. No single site can be scaled up to meet a production target as it will have requirements in terms of calf or maize inputs, or not produce the same currency (finished cows) as the production target.

In this chapter, therefore, I fit density-yield functions in order to investigate the effects of yields on species' population densities within individual sites. This allows me

to compare my results with those from elsewhere but I do not use them to estimate regional population sizes. Instead I use the land-use scenarios described in Chapter 5 to do this.

## 4.2 Methods

### 4.2.1 Estimating yields of study sites

To estimate study site yields I multiplied the area of each land use in a site by its yield, estimated in Chapter 3: grazing yield for grazed land uses and maize and fodder grass yields. This gave me site totals for kilograms of calf protein, kilograms of finished cow protein and tonnes of maize equivalents.

#### Converting yields to a single currency

To compare sites I converted all production to a single metric: ‘finished cow equivalents’. I multiplied calf protein production by the calf conversion ratio: the kilograms of finished cow protein eventually produced for each kilogram of calf protein (see Section 3.2.3). I multiplied the tonnes of maize equivalent produced by the feed conversion ratio for finishing ranches: the kilograms of finished cow protein produced by feeding animals one tonne of maize equivalent (see Section 3.2.2). Once all production values were in kilograms of finished cow protein, I summed them and divided by the area of each study site (100 ha) to get yield, measured in a common currency across all sites.

### 4.2.2 Fitting density-yield functions

I used maximum-likelihood optimisation to fit two possible density-yield functions. Model (1) is monotonic, whereas Model (2) allows populations densities to increase and then decrease:

$$(1) : \quad n/v = \exp(b_0 + b_1 x^\alpha)$$

$$(2) : \quad n/v = \exp(b_0 + b_1 x^\alpha + b_2 x^{2\alpha})$$

where:

$n$  = the number of clusters observed in the study site

$v$  = an offset term to adjust for the area surveyed

$x$  = the yield of the site in kilograms of protein per hectare per year

For birds,  $v = \sum A_i/s$ , where:

$A_i$  is the effective detection area for the species at point  $i$ , derived from detection functions (see Section 2.3.2) and summed across all points surveyed in the site;  $s$  is the mean cluster size for the species.

For trees,  $v$  is the total area surveyed in the site.

For dung beetles, we did not know how large an area we effectively surveyed, as the distance that beetles travel to dung is not certain. I therefore used the number of traps in a site (after accounting for those destroyed by animals) as an offset term which adjusted for inter-site variation in sampling effort (see Section 2.3.2).

Following Phalan et al. (2011b) I constrained the value of  $\alpha$  to be positive and less than 4.58. Values above this give similarly shaped curves with very similar likelihoods, making it impossible to pick a maximum likelihood model.

I fitted models using the constrained optimisation function `ConstrOptim` in R (R Core Team, 2015) modifying a script written by Anthony Lamb (Kamp et al., 2015). `ConstrOptim` is sensitive to starting parameters, so I first fitted ordinary least squares regressions for the two models, varying  $\alpha$  from 0.1 to 4.58 and selecting the version of each model with the smallest residual sum of squares. I then used the values for  $b_0$ ,  $b_1$ ,  $b_2$  and  $\alpha$  from these models as my starting values in `ConstrOptim`. I plotted models' predictions for yields from zero to 125% of the maximum estimated yield to allow for the possibility of future yield increases. I considered estimated population densities greater than 150% of the highest observed density to be unrealistic and when models predicted these I used the function `ConstrOptim.nl` from the package `{alabama}` to fit models using maximum-likelihood with a non-linear constraint.

I calculated the models' residual deviances (multiplying log likelihood by -2) and selected Model (1) for reasons of parsimony, unless Model (2) had a residual deviance more than 3.84 lower (critical  $\chi^2$  value for one degree of freedom at  $p = 0.05$ ).

I did not fit density-yield functions to species only found in zero-yielding baseline sites and instead assumed population densities of zero at all yields above zero.

### 4.2.3 Categorising species' responses

I categorised species' responses based on their predicted population densities at different target yields.

#### Setting target and permissible yields

I defined each target yield as the mean yield across a region; this could be met by a range of land-use strategies. For example a target yield of 100 kg ha<sup>-1</sup> could be met



by farming the whole region at  $100 \text{ kg ha}^{-1}$ , or 25% of the region at  $400 \text{ kg ha}^{-1}$ . I set the minimum target at an arbitrarily low level and the maximum as 125% of the maximum observed yield for my study sites.

Not all land-use strategies can meet every target yield. The lowest permissible yield is equal to the target (i.e. farming all available land at that yield) and I termed this strategy ‘land sharing’. The maximum permissible yield was always 125% of the maximum I recorded at my sites. I termed farming at this yield ‘land sparing’ and all other yields ‘intermediate strategies’. For each target-strategy combination I assumed all agricultural land was farmed at the same yield.

### Estimating population densities in agricultural land and natural habitats

I used the best-fit density-yield function for each species to predict its population density in both the agricultural land and natural habitats for every target yield and land-use strategy. I then weighted these densities by the proportion of a region under each land use to get a mean density across the region. Using the example above, with a target of  $100 \text{ kg ha}^{-1}$ , a species’ mean density under land sharing would be the predicted density at  $100 \text{ kg ha}^{-1}$ . With a yield of  $400 \text{ kg ha}^{-1}$ , however, the mean density would be:

$$D_{mean} = \frac{1}{4}D_{400} + \frac{3}{4}D_{baseline}$$

where:

$D_{mean}$  = mean population density of the species across the region

$D_{400}$  = population density of the species in agricultural land with a yield of  $400 \text{ kg ha}^{-1}$

$D_{baseline}$  = population density of the species in natural habitats

### Picking best strategies and categorising species

For each target yield, I calculated the land-use strategy (land sharing, land sparing, or an intermediate strategy) that resulted in the highest mean density of each species. If the mean density under this strategy was higher than in baseline natural habitats I classified the species as a ‘winner’, if lower I classified it as a ‘loser’.

Species were therefore assigned to one of six categories for each target yield: winners favoured by land sharing, an intermediate strategy, or land sparing; or losers that do least badly with land sharing, an intermediate strategy, or land sparing. Some species remained in the same category for all target yields, whereas the shapes of the

density-yield functions meant that some species changed categories as target yields increased.

#### 4.2.4 Testing the sensitivity of my results

To test the sensitivity of my results to the inclusion of species with few records I performed analyses on all species, and on a subset excluding species with fewer than 10 records. This restricted analysis is likely to give a more conservative estimate of the benefits of land sparing, because many rare species were found largely or exclusively in zero yielding baseline sites. It ensures, however, that my results show genuine patterns of population densities, rather than simply reflecting poorly sampled biodiversity.

#### 4.2.5 Predictors of species' responses

For each taxon I tested a range of possible variables to explore co-variables of species' responses to agricultural yields. I sorted species into five groups – species that were always winners irrespective of target yield; consistent loser species that always fared least badly under land sharing, land sparing, or intermediate strategies; and species with variable responses, including those that were always losers but that were favoured by different strategies at different target yields. I then used Fisher's exact tests (because of low expected values, Crawley 2005) to see if the distribution of species amongst categories was independent of each explanatory variable in turn.

For birds I tested associations with range size and forest dependence using the World Bird Database (BirdLife International, 2015) to classify species as having small or large global ranges and as being forest dependent or not. I classified species with an Extent of Occurrence greater than 270,000 km<sup>2</sup> as having 'large' global ranges, as this is approximately the size of the ecoregions that make up the Yucatán Peninsula (YP, Olson et al., 2001). For forest dependence, I combined the 'forest specialist' with the 'forest as a major habitat' category, and 'generalist' with 'non-forest' to leave simply 'forest dependent' and 'non-forest dependent' categories.

For trees I tested associations with range size and wood density. I used the *Flora Digital: Península de Yucatán* (CICY Herbarium, 2014) to classify species as having a small or large global range, depending on if they were restricted to Central America or not. I used wood specific gravity values from Zanne et al. (2009), classifying species as having high or low wood densities depending on whether they had densities higher or lower than the mean density for all species I surveyed, after excluding those without

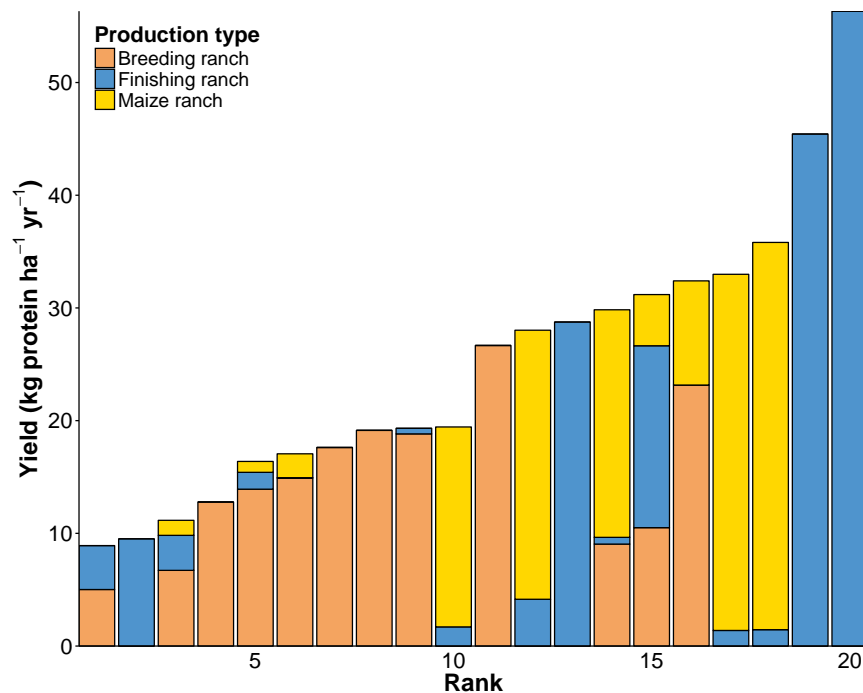
species specific values (see Section 2.4.2) and testing whether densities were normally distributed (Shapiro-Wilk test:  $W = 0.98$ ,  $p = 0.172$ ).

For dung beetles I looked for any association with body size (greater or less than 5 mm in length); diet (generalist, coprophage, or ‘trophic specialists’ - those that specialise on fruit or fungi Halffter and Halffter, 2009); dung removal strategy (tunneller or roller); and activity period (diurnal or nocturnal). Classifications for all but size came from Halffter and Matthews (1966); Hanski and Cambefort (1991); Navarrete and Halffter (2008) and Barragán et al. (2011).

## 4.3 Results

### 4.3.1 Yields of study sites

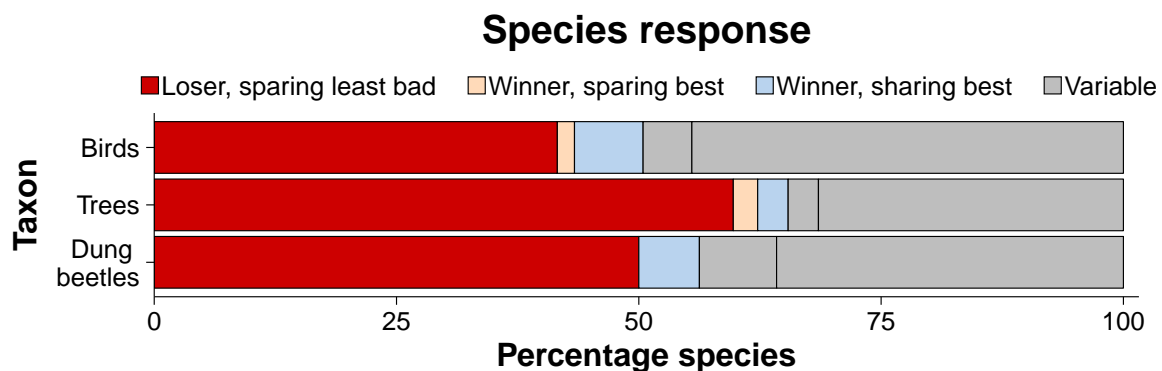
The highest yielding sites were *tecnificado* sites that produced finished cows and maize; breeding ranches tended to have lower yields (Fig. 4.1).



**Fig. 4.1** Yields of my productive study sites, showing the contribution of different production types.

### 4.3.2 Species responses

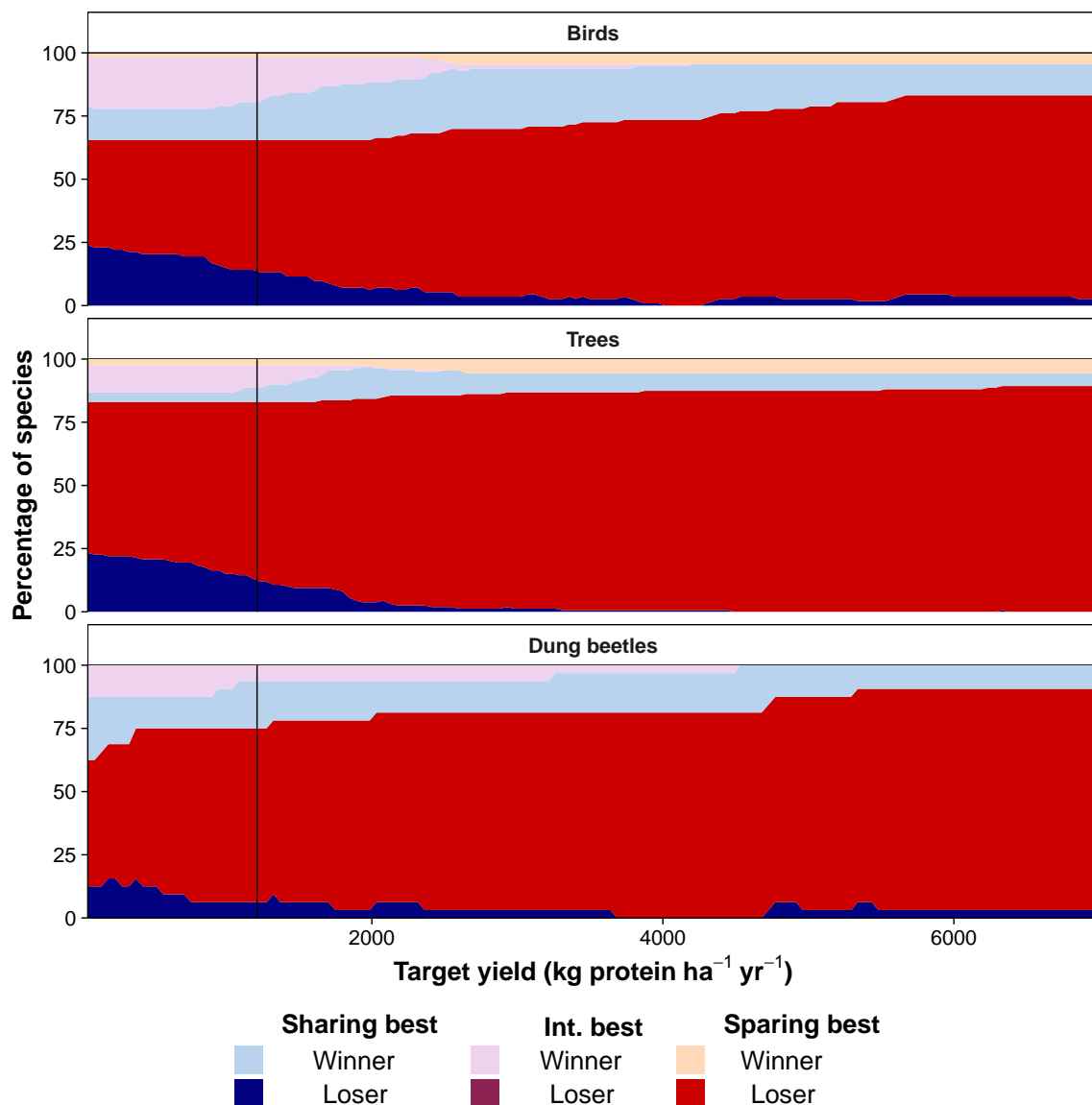
The largest response category for each taxon was losers that did least badly with land sparing (Fig. 4.2). For trees and dung beetles most species belong to this group at all target yields and the proportion of species in this group increased as the target yield increased (Fig. 4.3). Birds had a higher proportion of winners than did trees or dung beetles, with the majority of winner birds favoured by land sharing. Across all 305 species analysed, no species were losers favoured by land sharing at all target yields. Between 33% (trees) and 44% (dung beetles) of species had optimal strategies that varied as the target yield increased, with most becoming losers that did least badly with land sparing (Fig. 4.3). Removing rare species did not alter the patterns observed (Figs. A.2, A.3).



**Fig. 4.2** The proportion of species in each taxon in different response categories. Black lines show the number of species that are always winners, but which are favoured by different strategies at different target yields.

### 4.3.3 Predictors of species' responses

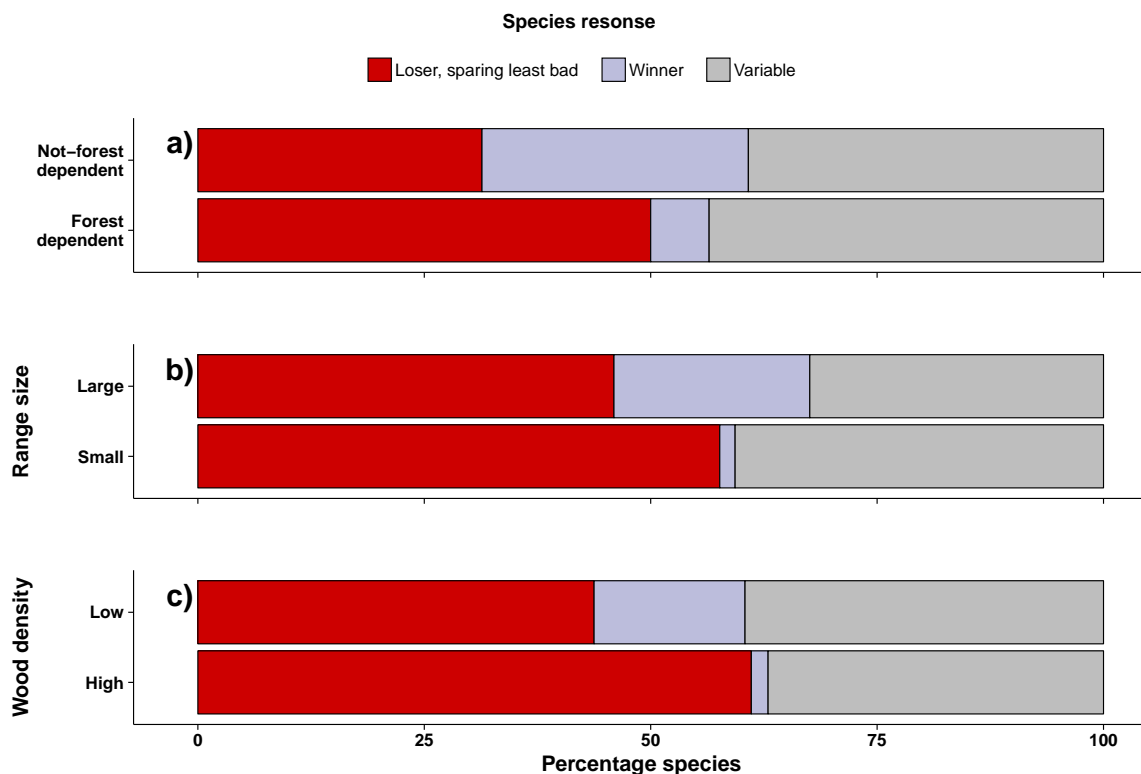
There was a significant difference in response categories for birds with different levels of forest dependence ( $p=0.004$ ) and for trees with different range sizes ( $p=0.006$ ) or wood densities ( $p=0.017$ , Fig 4.4). No other variables predicted species' response categories (birds - range size:  $p=0.79$ ; dung beetles - size:  $p=0.22$ ; dung removal strategy:  $p=0.40$ ; activity period:  $p=0.18$ ; diet:  $p=0.19$ ).



**Fig. 4.3** Response categories of birds trees and dung beetles at different target yields. Light colours are winners, dark colours losers. The vertical black lines represents current yield: the production in Tizimín District of calves, finished cows and irrigated maize grain, converted to finished cow equivalents and divided by the land available for production.

## 4.4 Discussion

Most species of birds, trees and dung beetles in Tizimín District are highly sensitive to agriculture. Whilst most species decline with increasing yields, it is the initial transition from natural habitats to agricultural land that causes the greatest declines in



**Fig. 4.4** Variations in species' responses to agriculture with different explanatory variables for **a)** forest dependence in birds ( $p=0.004$ ) **b)** global range size ( $p=0.006$ ) and **c)** wood density in trees ( $p=0.017$ ). All values are from two-sided Fisher's exact tests. The 'winners' category contains all winner species, irrespective of optimal land-use strategy.

population densities. These results are robust to excluding rare species, demonstrating that they do not depend on very rare, or poorly sampled species. These findings re-emphasise the importance of natural habitat protection as a key conservation strategy for the biota of the YP.

#### 4.4.1 Comparisons between taxa and with previous studies

My results are consistent with previous studies in a range of ecological and agricultural systems across the world (Phalan et al., 2011b; Hulme et al., 2013; Edwards et al., 2014, 2015; Dotta et al., 2015; Kamp et al., 2015; Feniuk, 2016). Most species are losers favoured by land sparing, and patterns across taxa are similar: plants are more sensitive to agricultural disturbance than other taxa (Phalan et al., 2011b; Dotta, 2013; Feniuk, 2016), reflecting their sessile nature and the fact that the transition from natural habitats to agricultural land is often accompanied by the wholesale replacement

of native vegetation. Dung beetles were also extremely sensitive to agricultural change, possibly reflecting their sensitivity to small changes in habitat structure (Halffter et al., 1992; Halffter and Arellano, 2002), or the reliance of some species on specific types of dung (but see Larsen et al., 2006).

The relative resilience of birds to agricultural change (again supporting Phalan et al., 2011b; Dotta, 2013; Feniuk, 2016) could be because they can move between patches of remnant vegetation within agricultural landscapes more easily than can other taxa. This high mobility may also have allowed species resilient to agriculture to expand into new regions alongside farming, thus shifting the avifauna I sampled towards more agriculturally tolerant species than might have been present prior to the advent of farming.

The relative insensitivity of birds to agricultural change raises questions over their suitability as indicators of wider biodiversity or ecological change. However, a large analysis of the use of different species groups as indicators in the Brazilian Amazon found that not only were birds one of the most cost-effective taxa to survey, but they were also very good indicators of ecological change, and better than average indicators of biodiversity change (Gardner et al., 2008). Indeed, despite their relative resilience, losers that did least badly with land sparing still comprised the largest group of bird species. This increased to an overall majority at relatively low yields.

#### 4.4.2 Predictors of responses

A higher proportion of forest dependent than non-forest dependent bird species were losers that did least badly with land sparing (Fig. 4.4): many forest-dependent species such black-faced antthrush *Formicarius analis* and ivory-billed woodcreeper *Xiphorhynchus flavigaster* have very low population densities on any agricultural land; their mean population density will therefore depend largely on the proportion of the region under natural habitats and so they will do least badly under land sparing. Conversely, more non-forest dependent species were winners because species such as blue-black grassquit *Volatinia jacarina* and Botteri's sparrow *Peucaea botterii* rely on open habitats which increase in extent under agricultural expansion.

For trees with large global ranges, a higher than expected proportion were winners, and fewer were losers that did least badly with land sparing (Fig. 4.4). This follows previous results for trees (Phalan et al., 2011b) and birds (Phalan et al., 2011b; Hulme et al., 2013) in Ghana, Uganda and northern India, and may reflect the fact that more widespread species are likely to have wider fundamental niches (Morin and Chuine, 2006) and may therefore may be more resilient to habitat disturbance than more

specialised, range restricted species. Higher wood density species tend to grow more slowly (King et al., 2006) and as such may be more sensitive to habitat disturbance than are faster-growing opportunistic species; this would explain why a higher proportion of densely wooded species were losers that did least badly with land sparing.

Previous studies have suggested that body size and activity period could be important in determining dung beetle response to environmental change (Jankielsohn et al., 2001; Larsen et al., 2005; Gardner et al., 2007; Larsen et al., 2008; Nichols et al., 2013) but my results did not support this. This could be due to the lack of detailed studies of Yucatecan dung beetle communities, a general lack of knowledge of dung beetle functional traits (Nichols et al., 2013), the relatively small number of species collected, or the broad categories I used to classify species. For example, my 'coprophage' classification included species such as *Canthon indigaceus* which were hyperabundant in cattle pastures, but some coprophages may rely on the dung of one or two species and thus be extremely sensitive to ecological change (e.g. Nichols et al., 2009). Exactly what determines how Scarabaeinae species respond to agricultural yields is far from clear and, given their functional importance in cattle pastures, this should be a research priority for both conservationists and rangeland managers.

#### 4.4.3 Limitations of this analysis

As discussed previously, the results from this chapter cannot be used to predict actual species populations under different food-production scenarios. The highest yielding study sites (i.e. those that would be used in a land-sparing strategy) were dominated by finishing and maize ranches (Fig. 4.1). These sites require breeding ranches to supply them, and so farming all agricultural land in a region at this yield would require a large area elsewhere to supply these. Similarly, the lowest yielding sites (i.e. those that would form a land sharing scenario) are largely breeding ranches that require finishing ranches to fatten the calves produced into slaughter-ready cows. To account for these agricultural footprints I developed a method to construct plausible scenarios for Yucatecan livestock production, described in Chapter 5.

In addition, for some species I had records from very few sites (Table A.1) which is likely to have made model fitting somewhat unreliable. Whilst dropping rare species (Figs. A.2, A.3) will have accounted for this to some extent, results from density-yield functions fitted to few non-zero densities should be interpreted with caution.



## 4.5 Conclusions

Despite its limitations, this analysis demonstrates that birds, trees and dung beetles in Tizimín District respond in a similar manner to increasing agricultural yields as a range of taxa from across the world (Phalan et al., 2011b; Dotta, 2013; Hulme et al., 2013; Edwards et al., 2014; Dotta et al., 2015; Edwards et al., 2015; Kamp et al., 2015; Feniuk, 2016). This is despite the very different production systems studied and the the long history of anthropogenic and natural disturbance in the YP. I had expected that the combination of agricultural clearance and the evolutionary history of the region would have acted as an extinction filter, leading to the loss of the most disturbance sensitive species (Balmford, 1996) and the evolution of a biota which was relatively resilient to habitat disturbance, hurricanes and periodic droughts (Hodell et al., 1995; Boose et al., 2003; Haug et al., 2003). I discuss these results more fully and in comparison with those obtained from scenario building in Chapter 7.



## CHAPTER 5

### FUTURE SCENARIOS

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*“We have inherited an incredibly beautiful and complex garden, but the trouble is that we have been appallingly bad gardeners. We have not bothered to acquaint ourselves with the simplest principles of gardening”*

Gerald Durrell

#### 5.1 Introduction

Density-yield functions provide us with valuable information about how species respond to increasing yields, but to assess how regional populations would change under different land-use approaches I needed land-use scenarios that can take into account the external requirements of different study sites: maize fodder, calves, and finishing ranches to turn calves into finished cows. Such scenarios are not predictions of what will happen in Yucatán, but rather tools for investigating how choices over land uses are likely to affect biodiversity.

### 5.1.1 Definitions

In this chapter I use the following terms:

- **Production target:** the overall production of animal protein (as finished cow, calf or both) for the region.
- **Land-use strategy:** whether agricultural land is farmed at the highest possible yield (land sparing), the lowest possible yield (land sharing), or an intermediate yield.
- **Land-use scenario:** the unique combination of production target and land-use strategy.

### 5.1.2 Aims of this chapter

In this chapter I model different possible land-use scenarios for Tizimín District (TD) up to 2030, quantify the land uses in each and assess their probable effects on population sizes of birds, trees and dung beetles. To do this, I need to:

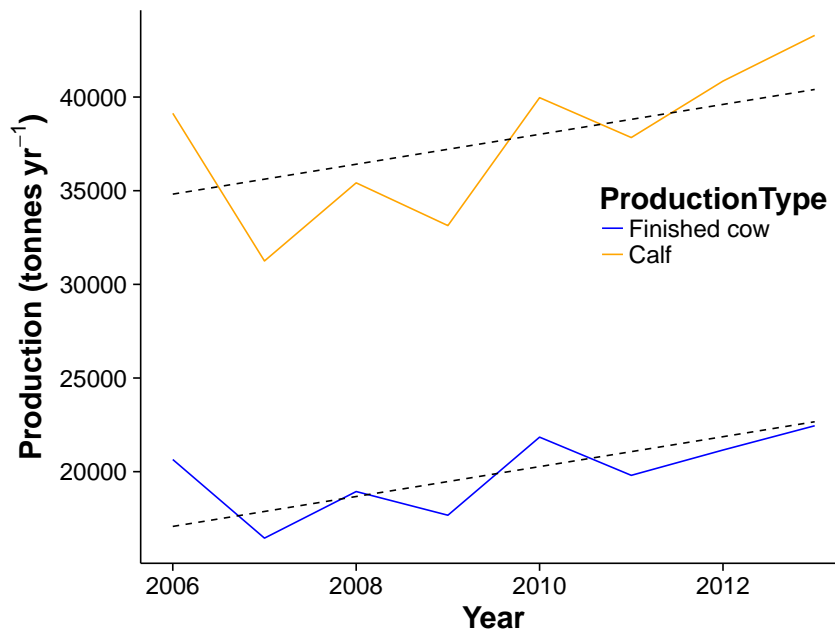
1. Choose plausible production targets.
2. Estimate the production and input requirements of each study site in terms of maize equivalents, calf protein and finished cow protein.
3. For a given production target, build up a land-use scenario by randomly picking study sites that reflect a land-use strategy (say, land sharing) until the production target and associated maize and calf requirements are met.
4. Repeat this for different land-use strategies (using different groups of study sites).
5. Repeat Steps 3 and 4 for other production targets.
6. Combine species' population densities in different study sites with the land-use scenarios generated by Steps 3 to 5 to estimate their consequences for the region's bird, tree and dung beetle populations.

## 5.2 Picking plausible futures

TD produces both finished cows and calves for export, so I set production targets for both. I used data from SAGARPA (2015) for 2006–2013 (the last year for which data were available) and backwards stepwise model selection to construct a linear model

relating animal production to year, whether the output was of finished cows or calves, and an interaction between year and output type. Both year and production type were significant (Fig. 5.1), but not the interaction between the two ( $F_{1,12} = 0.973$ ,  $p = 0.343$ ).

I converted these production levels to production targets for protein using a dressing percentage of 50% (FAO, 1972) and a protein content for ruminant meat of 17.4% (USFDA, 2015). I estimated current production as the mean of the values for 2010–2013 and used my fitted linear model to project annual increases up to 2030. I estimated 2030 production levels as approximately 130% of current levels for calves, and 170% for finished cows. However, to account for the uncertainty in future production patterns I used targets ranging from 10 to 170% of current production. For each production target I increased the production of calves and finished cows at the same rate.



**Fig. 5.1** Production levels for calves (gold) and finished cows (blue) in Tizimín District for 2006–2013. Dashed lines show the relationship estimated by linear regression: Calves:  $Production = 798 \times year - 1566664$ ; Finished cows:  $Production = 798 \times year - 1584404$  ( $F_{2,13} = 92.1$ ,  $r_{adj}^2 = 0.924$ ,  $p < 0.0001$ )

I assumed that TD produced all the maize required within the region. This is not the situation today (the region imports the majority of maize used from the USA and elsewhere), but the area of irrigated maize for cattle fodder is increasing (Fig. 1.4) and this assumption allows me to quantify the biodiversity impacts of fodder production. I explore the effects of relaxing this assumption in Section 5.7

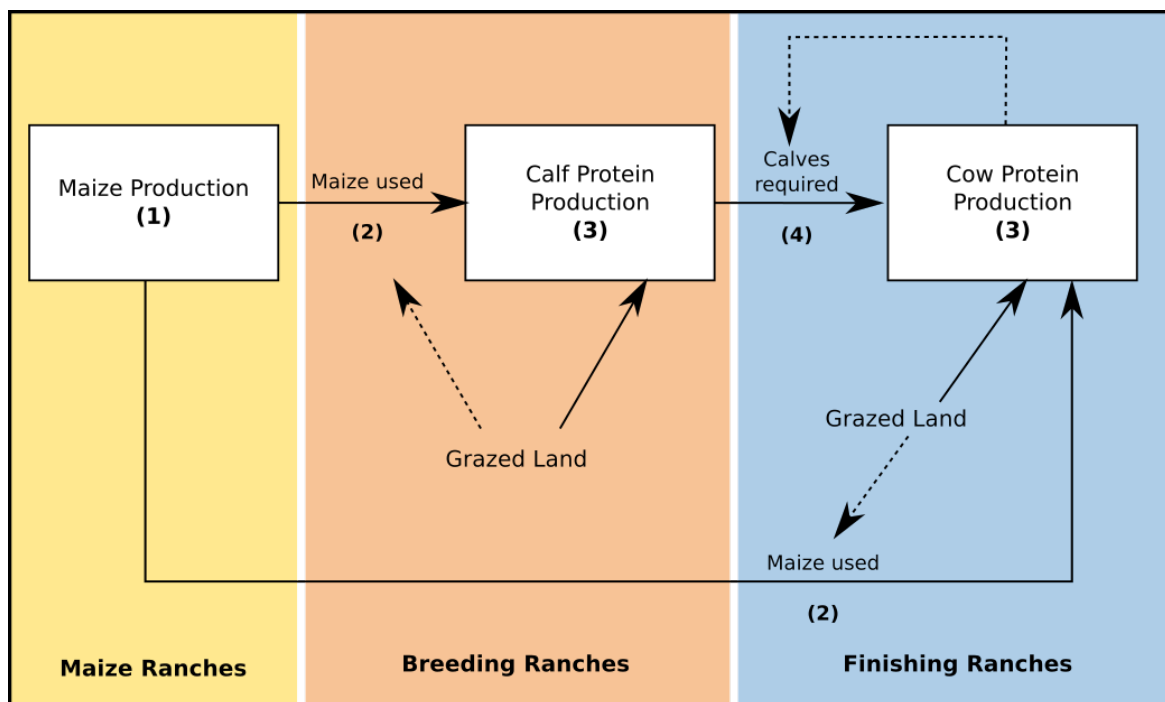
## 5.3 Building scenarios

### 5.3.1 Estimating study site production and requirements

I estimated the production and requirements of each of my study sites using the procedure in Fig 5.2:

- (1) I calculated the production of maize equivalents in each site by multiplying the area of maize and fodder grass by their yields (estimated in Section 3.2.1).
- (2) I calculated the maize use of the breeding and finishing ranches in each site by multiplying the area of each type of grazed land by the coefficients from the Maize Use Model (Section 3.2.4).
- (3) I calculated the production of calf and finished cow protein in a site:
  - (a) Production from grazing: I multiplied the area of each type of grazed land in breeding and finishing ranches by its grazing yield (from the Protein Production Model, Section 3.2.2).
  - (b) Production from maize: I multiplied the maize used (from Step 2) by the feed conversion ratio for breeding or finishing ranches (i.e. the kilograms of calf or cow protein produced for each tonne of maize used as feed, again from the Protein Production Model in Section 3.2.2.).
  - (c) I summed the values from (a) and (b) to get the overall production of calf or finished cow protein in each site.
- (4) I estimated the calves required by finishing ranches by multiplying the overall production of cow protein (from Step 3) by the calf requirement ratio (from Section 3.2.3). *Completo* ranches produce their own calves and so I set their calf requirements to zero.

Finally, I estimated the total production of each site and the net production of maize equivalents and calf protein. I converted all values into finished cow equivalents using the feed conversion ratio for finishing ranches (from the Protein Production Model, Section 3.2.2) and the calf conversion ratio (from Section 3.2.3). I then summed these to obtain total production of a site. Net production of maize equivalents was the site's production of maize equivalents minus its usage; net calf production was the site's production of calf protein minus the calves required (again, with all values converted to finished cow equivalents).



**Fig. 5.2** Schematic of the ranching system in Yucatán. Solid lines represent energy or biomass flows; dashed lines show that information on the grazed land in a ranch is needed to estimate maize use and that calf requirements depend on cow protein production. Numbers refer to the calculation steps in Section 5.3.1.

### 5.3.2 Scenario building method

I first grouped sites based on production type and yield and then used these groups to iteratively build land-use scenarios to meet a range of production targets.

#### Grouping study sites by production type and yields

To group my study sites I classified them into different production types and ranked them by yield. I classified the five zero-yielding forest sites as baselines; the five maize ranches as maize sites; and the remaining sites as breeding or finishing sites based on whether they had a greater net production of calf or finished cow protein.

To calculate each site's yield I divided its total production by the area required to produce it. If the site had negative net maize production, then the area required was the size of the site (100 ha) plus the value of this deficit divided by a yield of 8 t ha<sup>-1</sup>. Otherwise the area required was simply the area of the site. After calculating yields I ranked sites within the breeding, finishing and maize classifications and grouped subsets of each into different land-use strategies, based on their yields (Table 5.1).

**Table 5.1** How I grouped study sites into land-use strategies for scenarios. Sh. and Sp. refer to land sharing and land sparing, Br, F and M refer to breeding, finishing and maize sites. Yields are in kilograms of finished cow equivalents.

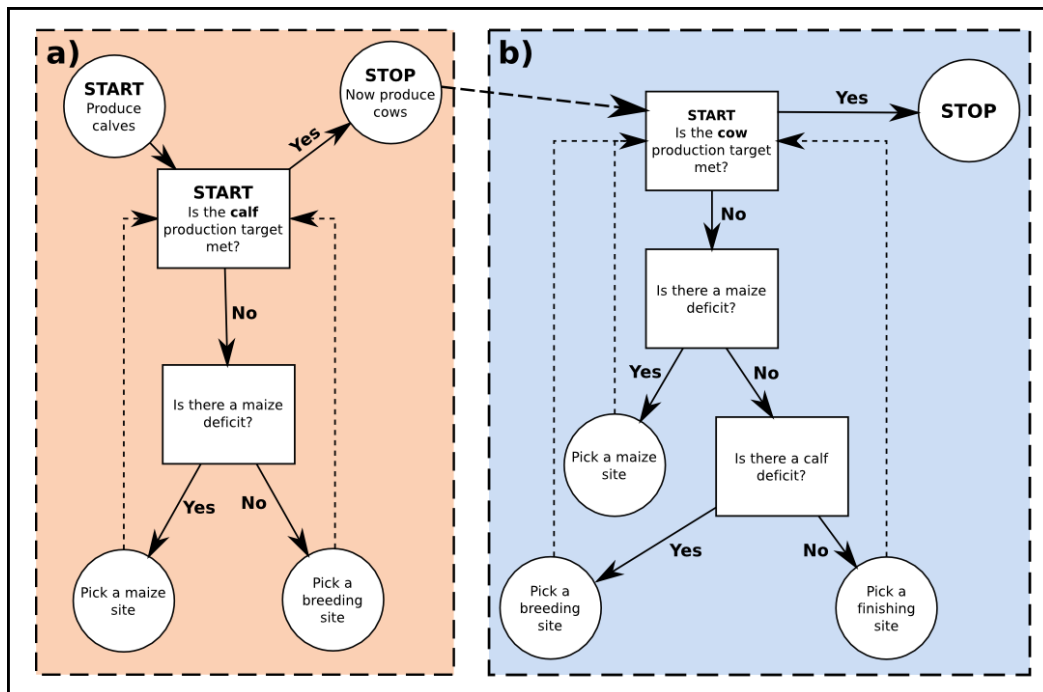
Site	Yield (kg ha <sup>-1</sup> yr <sup>-1</sup> )	Rank	Land-use strategy					
			Sh.	Intermediate			Sp.	
Br1	1269	8	✓	-	-	-	-	-
Br2	1712	7	✓	✓	-	-	-	-
Br3	1722	6	✓	✓	✓	-	-	-
Br4	1745	5	-	✓	✓	✓	-	-
Br5	1894	4	-	-	✓	✓	✓	-
Br6	2022	3	-	-	-	✓	✓	✓
Br7	2617	2	-	-	-	-	✓	✓
Br8	3251	1	-	-	-	-	-	✓
<hr/>								
F1	1151	7	✓	-	-	-	-	-
F2	1934	6	✓	✓	-	-	-	-
F3	2664	5	✓	✓	✓	-	-	-
F4	2854	4	-	✓	✓	✓	-	-
F5	3326	3	-	-	✓	✓	✓	-
F6	4545	2	-	-	-	✓	✓	✓
F7	5553	1	-	-	-	-	✓	✓
<hr/>								
M1	2666	5	✓	✓	✓	-	-	-
M2	3248	4	✓	✓	✓	✓	-	-
M3	3791	3	-	✓	✓	✓	✓	-
M4	3899	2	-	-	✓	✓	✓	✓
M5	4266	1	-	-	-	✓	✓	✓

### Building the scenarios

For each production target from 10–170% of current production I used the process outlined in Fig. 5.3 to build land-use scenarios using the sites from one land-use strategy. I first picked study sites to produce calves for export and the maize to support this production (Section a) of Fig. 5.3).

1. I randomly selected a breeding site and evaluated whether its net calf protein production was greater than the production target for calf protein. If so, I stopped and moved to Section b) below. If not, I moved to Step 2.
2. I evaluated whether the net maize production of the selected site(s) was negative (i.e. if there was a maize deficit). If so, I moved to Step 3, if not then Step 4.
3. I randomly selected a maize site, added it to the list of selected sites, and returned to Step 2.
4. I randomly selected another breeding site, added it to the list of selected sites, and repeated Steps 2-4 until the production target for calf protein was met.





**Fig. 5.3** Schematic of scenario building process, starting by **a)** meeting the calf protein production target and then **b)** the finished cow production target.

This process produced calf protein for export, the maize to support this production and some finished cow protein (some breeding sites also produced small amounts of finished cow protein). I evaluated whether this satisfied the production target for finished cow protein and stopped the scenario building process if so. If not, I continued with Section b) of Fig. 5.3.

1. I randomly selected a finishing site, added it to the list of selected sites, and moved to Step 2, below.
2. I evaluated whether there was a maize deficit. If so I then moved to Step 3, if not then Step 4.
3. I randomly selected a maize site, added it to the list of selected sites, and returned to Step 2.
4. I evaluated whether, once accounting for the calf production target, the selected sites had a calf deficit. If so then I randomly selected a breeding site, added it to the list of selected sites, and returned to Step 2. If not, I moved to Step 5.
5. I evaluated whether the finished cow protein production from all selected sites met the production target for cow protein. If so I then I stopped, if not, I returned to Step 1.

Because the scenario building process selected sites at random, repeating the process gave slightly different results. I therefore repeated the process multiple times for every scenario and used the mean number of times that each site was picked across these repeats for further analysis. I used bootstrapping to judge how many repetitions were needed by selecting, at random and with replacement, 1,000 runs of the analysis and calculating the mean and standard deviation of the number of times each site was selected across these runs. I then increased the sample size to a maximum of 150 runs, repeating the bootstrapping each time. From looking at how the mean and standard deviation varied with sample size I estimated that running the analysis 50 times would give sufficiently reliable results (Fig. A.4).

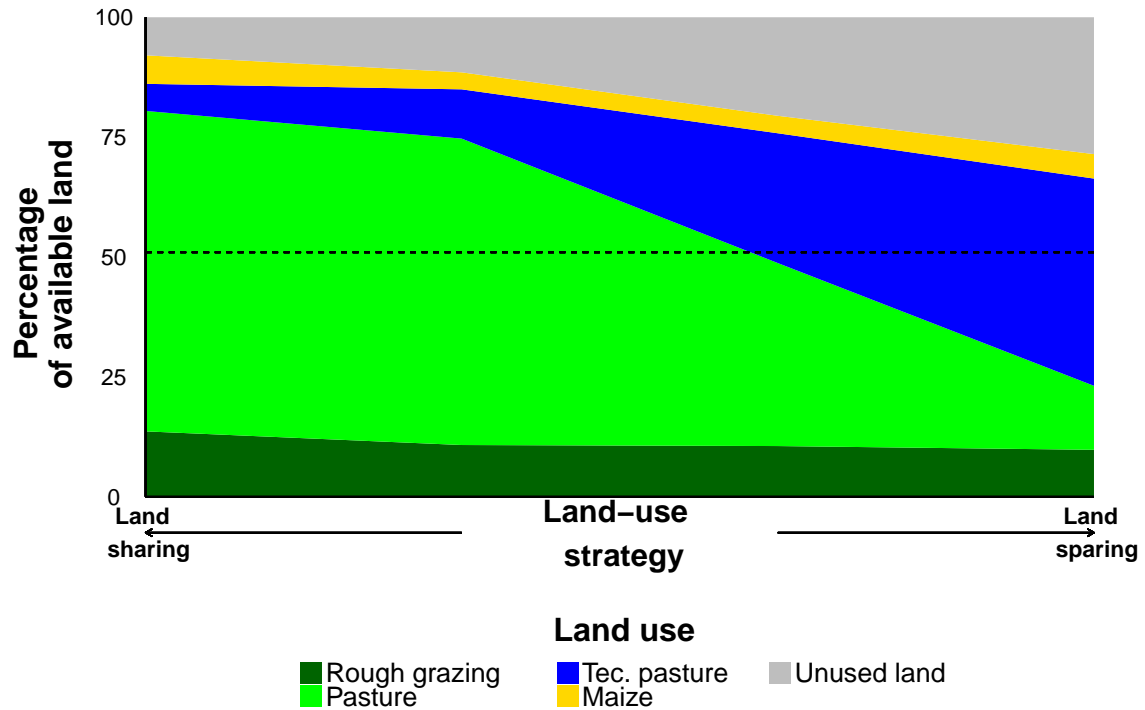
To test the sensitivity of my results to uncertainty in yield estimates, I also built scenarios using the lower estimate for maize and fodder grass yields of 3.02 t maize equivalents  $\text{ha}^{-1} \text{yr}^{-1}$  (see Section 3.3.1). I also used the 10,000 bootstrapped yield estimates derived in Section 3.2.6 to calculate 10,000 estimates of each site's production and requirements. I re-grouped sites into land-use strategies for each of these estimates, calculated how many times each site was used in each land-use strategy and compared these groupings to those I used to build my scenarios. Considerations over computing time prevented me from running the full scenario building process for the 10,000 repetitions.

## 5.4 Results: Land-use composition across different strategies

This process gave me land-use scenarios that met production targets from 10–170% of current production, using a range of land-use strategies. However, not all scenarios were feasible because some strategies required more land than was available in TD. I discarded these unfeasible scenarios, meaning that the study sites and land uses used in land sharing (i.e. the lowest yielding strategy) varied as production targets increased. Moreover, at a production target of 170% of current production levels, only land sparing was feasible. This in itself is informative but prevented me from comparing different land-use strategies. For further analyses I therefore assumed a 2030 production target of 130% of current production, equivalent to the likely production target for calf protein (see Section 5.2).

As the yields of land-use strategies increased, the area under technified pasture increased, and the area under pasture decreased (Fig. 5.4). The total area required also decreased – for example, at a production target of 130% of current production, the

total area required fell from 92% of available land under land sharing to 71% with land sparing. Using lower maize yields did not qualitatively change my results (Fig. A.5) and the bootstrapping exercise revealed that the majority of sites did not change grouping across most of the 10,000 repetitions (Fig. A.6). My results are therefore unlikely to change greatly even with uncertainty in yield estimates.



**Fig. 5.4** Area of different land uses under different land-use strategies for a 2030 production target of 130% of current production. Values are percentages of the total area of Tizimín District and the black dashed line shows the total area currently under pasture, technified pasture and maize (from SAGARPA, 2015). In reality, the area under production is larger than this because some of the forest and secondary regrowth in the region will be grazed. Unused land could in theory be spared for nature conservation.

## 5.5 Estimating the biodiversity impacts of scenarios

These scenarios provide estimates of the areas of different land uses under different strategies, but to assess which are the least damaging required information on their implications for biodiversity and carbon stocks. I describe their impacts on biodiversity below, and on carbon stocks in Chapter 6.

To investigate biodiversity impacts I estimated the pre-human and current populations of each species across the whole of TD and compared this with estimated regional populations under each scenario. I based all estimates on the population densities of each species in different study sites, which I estimated by dividing the total count of each species by the area surveyed in each site, taken from Section 2.3.

### 5.5.1 Estimating past and current population sizes

I assumed that before human arrival the region was completely forested and so estimated pre-human populations as the mean population density of each species across my five baseline study sites multiplied by the area of TD.

To estimate current population sizes I used a similar process to that used to build scenarios. I first used my quantitative interviews and agricultural ministry data for 2011 (the last year for which data were available, SAGARPA, 2015) to estimate the areas of pasture, technified pasture and cropland in TD. I assumed all cropland was maize although there are small areas of other crops. I estimated the area of rough grazing using National Institute of Statistics and Geography data on the area of secondary forest (INEGI, 2015), although not all of this is grazed. I then randomly picked study sites, with replacement, until the total area of each land use (pasture, technified pasture and cropland) in the selected sites equalled the total area of each land use in TD.

I then counted the number of times each study site was selected and multiplied this by each species' density in that site. Finally I summed these values across all study sites to get a regional population estimate.

As with the scenario-building process, because sites were selected at random, running the process multiple times will give different results. I therefore ran the site-selection process multiple times and took the mean number of times each site was selected across these. I used a bootstrapping approach to judge how many repetitions were needed: I selected, at random and with replacement, 1,000 runs of the analysis and calculating the mean and standard deviation of the number of times each site was selected across

these runs. I then increased the sample size, repeating the bootstrapping each time. I judged that 50 repeats would give sufficiently reliable results (Fig. A.7).

### 5.5.2 Estimating future population sizes

To estimate future population sizes for each scenario, I estimated each species' population size in agricultural land as the number of times each site was used in the scenario multiplied by the species' population density in the site. I then added this to its estimated population size in natural habitats: its mean population density in the five baseline sites multiplied by the area of land not required to meet the production target. For each production target I then identified the land-use strategy with the largest population size for each species and termed this the "optimal land-use strategy" for that species.

### 5.5.3 Classifying species responses

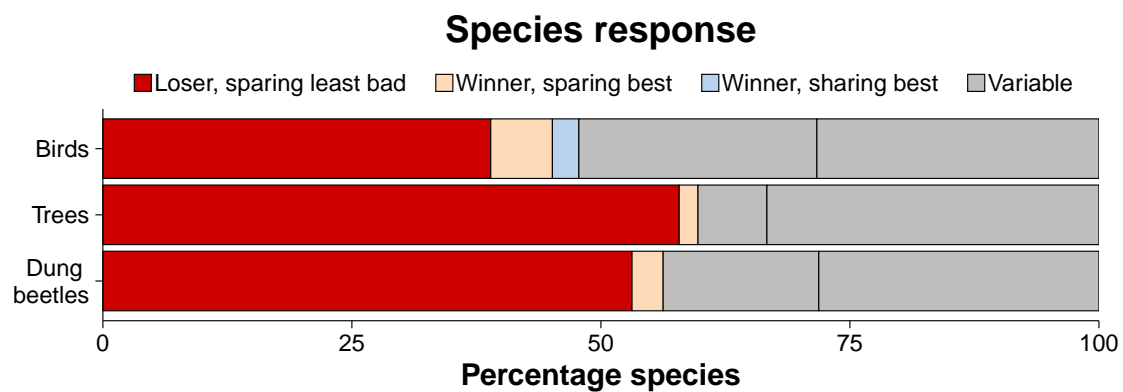
For each production target I classified each species' optimal land-use strategy as land sharing, land sparing, or an intermediate strategy, and each species as a winner or loser depending on whether its population size under its optimal land-use strategy was higher or lower than the pre-human population estimate. Species could therefore be classified as winners favoured by land sharing, an intermediate strategy, or land sparing; or losers that do least badly with land sharing, an intermediate strategy, or land sparing. For each species in each scenario I then calculated its population change relative to both the pre-human population and 2011.

To test the sensitivity of my results to the inclusion of rare species I performed analyses on all species, and on a subset excluding those with fewer than 10 records. Because many rare species were found largely or exclusively in zero yielding baselines, this restricted analysis may give a more conservative estimate of the benefits of land sparing. It does, however, ensure that my results show genuine patterns of population densities, rather than simply reflecting poorly sampled biodiversity.

## 5.6 Results: Biodiversity impacts of different land-use strategies

### 5.6.1 Species' classifications

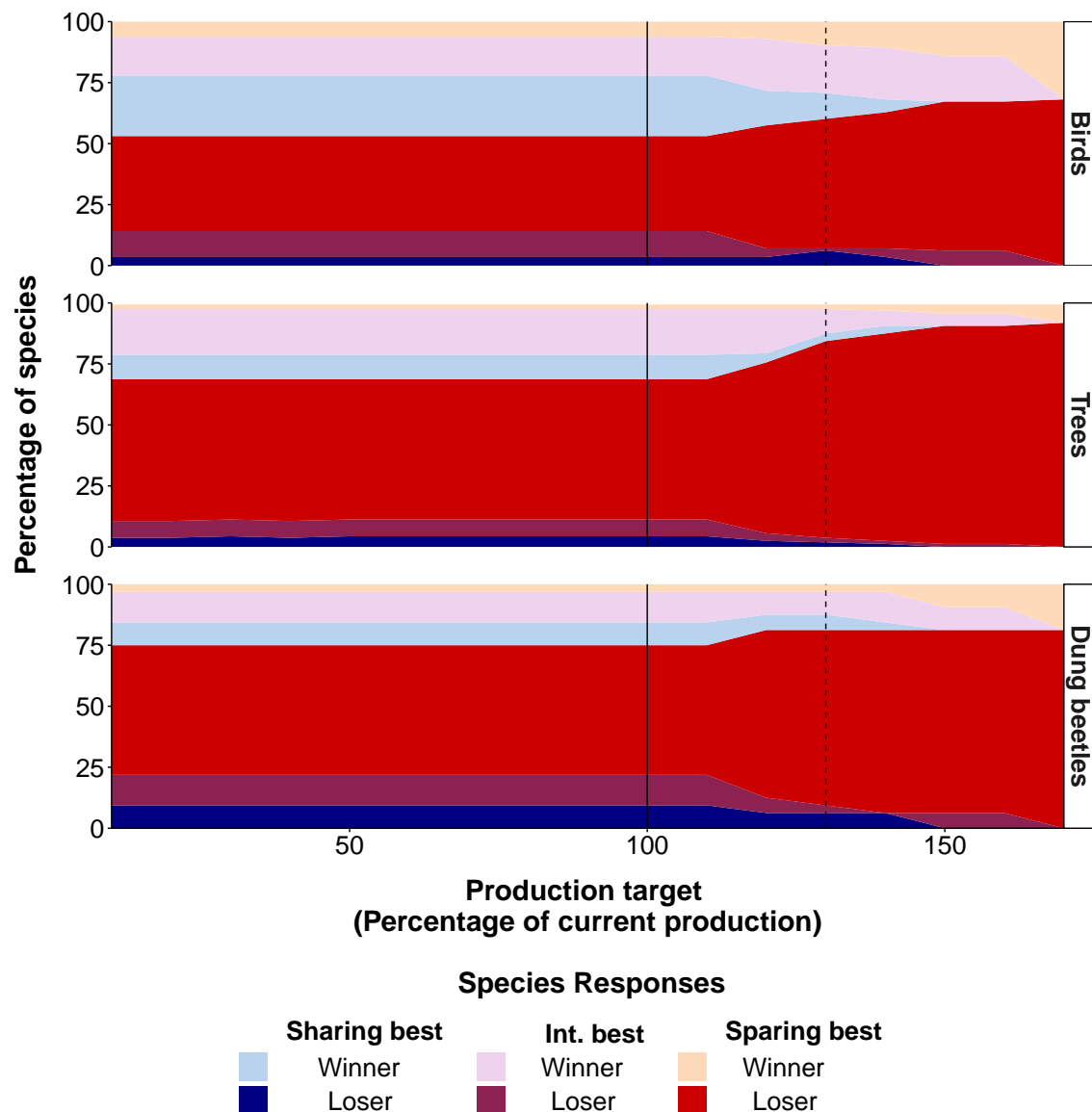
Across all production targets, more species were losers than winners with agriculture and more species did least badly with land sparing than with any other strategy (Fig. 5.5). More than 50% of tree and dung beetle species were losers that did least badly with land sparing, whereas a relatively large proportion of birds were winners. As production targets increased, more species of all taxa became losers that did least badly with land sparing (Fig. 5.6).



**Fig. 5.5** The proportion of species in each taxon with different optimal land-use strategies. Black lines show the number of species that are always winners, but which are favoured by different strategies at different production targets. Species with variable responses have maximum population sizes under different strategies, depending on the production target (see Fig. 5.6).

### 5.6.2 2030 population sizes

To investigate changes in population sizes I assumed a 2030 production target of 130% of current production. I analysed the 221 species that were losers in 2011 (i.e. those with estimated 2011 populations lower than their baseline populations, henceforth “2011 losers”) from the 83 that were winners (“2011 winners”). Almost all 2011 losers declined by 2030, relative to an all forest baseline, although declines were far less severe with land sparing (Fig. 5.7). Trees that were 2011 winners responded similarly, whilst 2011 winners in other taxa tended to increase, with no consistent patterns across land-use strategies. To calculate relative population sizes I excluded 60 species with



**Fig. 5.6** Proportion of species showing different responses to agriculture across all taxa and production targets. The solid vertical line shows current production levels, the dashed line a 2030 production target of 130% current production.

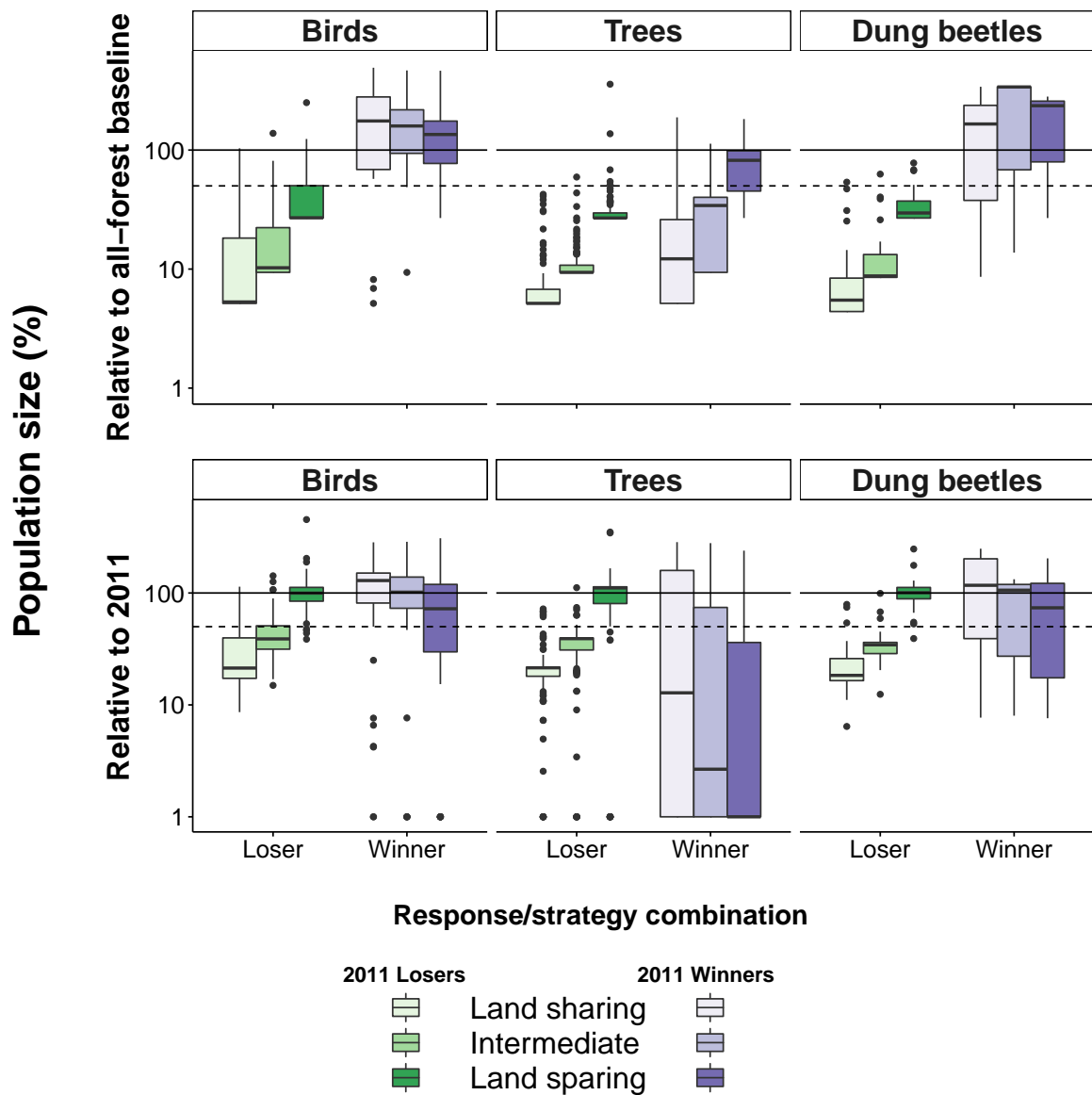
an estimated baseline population of zero, which could be recent arrivals to the region. Including these species by assuming an arbitrarily low baseline population size did not qualitatively alter my results (Fig. A.8).

Relative to 2011, most species declined by 2030, with far greater population declines under land sharing or intermediate strategies than land sparing (Figs. 5.7, 5.8). The only exceptions were birds and dung beetles that were winners in 2011, which showed

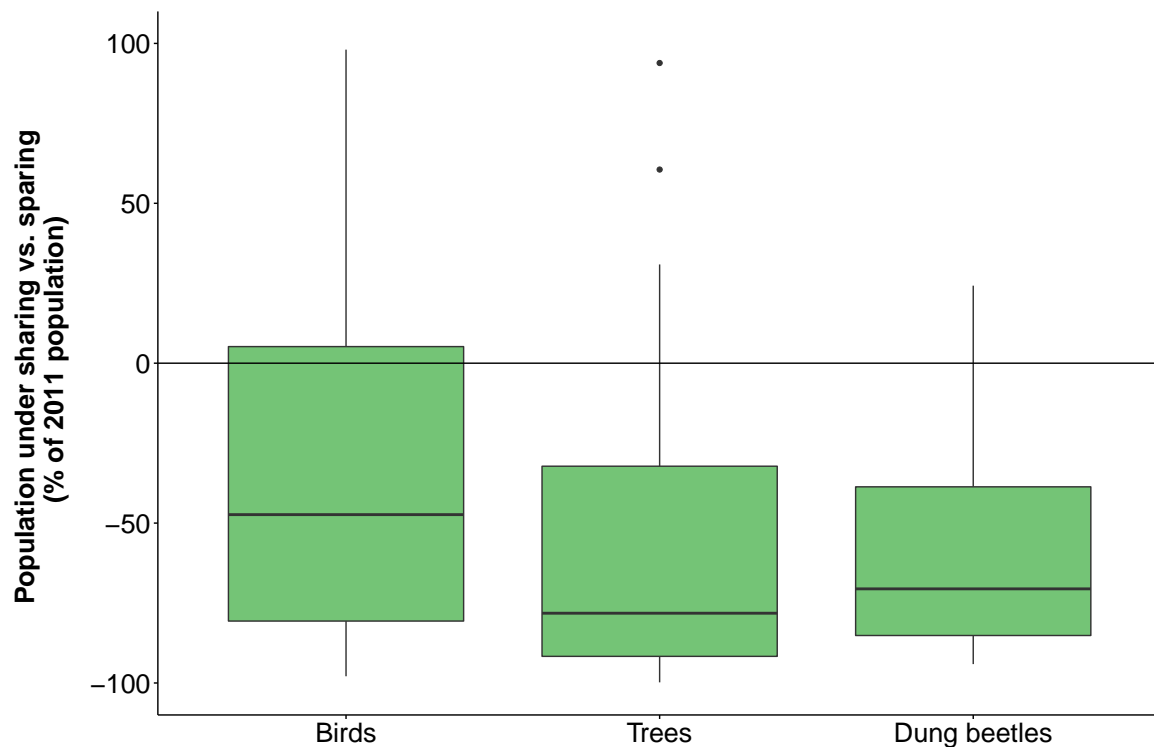
population increases with land sharing or intermediate strategies but declined with land sparing.

Dropping rare species did not qualitatively change my results in terms of species responses (Fig. A.9), or population changes (Figs. A.10, A.11). Similarly, using lower maize yields did not qualitatively change my results, although as a result of requiring larger areas under farming, 2030 population sizes tended to be slightly lower (Figs. A.12- A.14).





**Fig. 5.7** Estimated 2030 populations of birds, trees, and dung beetles relative to both an all-forest baseline and 2011 populations under different land-use strategies, assuming a 2030 production target of 130%. Horizontal lines show the median difference in population size; boxes the 1<sup>st</sup> and 3<sup>rd</sup> quartiles; and vertical lines 1.5 times the interquartile range. For clarity I have excluded 60 species with estimated baseline populations of zero and have used a logarithmic y-axis, truncated at 500% of baseline population sizes, although several species had larger relative populations. The solid horizontal shows a population of the same size, the dashed line shows a 50% decline.



**Fig. 5.8** Difference in 2030 population sizes of bird, tree and dung beetle species under land sharing compared to land sparing, assuming a 2030 production target of 130%. These are the same data as in Fig. 5.7, but with the difference between individual species' populations under different strategies shown. Horizontal lines show the median difference in population size, boxes the 1<sup>st</sup> and 3<sup>rd</sup> quartiles, and vertical lines 1.5 times the interquartile range. I have scaled population changes as percentages of 2011 population sizes.

## 5.7 Alternative production systems

TD currently produces calves for export as well as cows for slaughter, but both market forces and policy decisions may change this. Therefore, in addition to the “Business-as-usual” system described above, I modelled three alternative production systems. I selected these based on talking to ranchers and qualitative, semi-structured, interviews with key informants: the leaders of the two local cattle unions; researchers at the regional agronomic research station (two interviews); and local and state-level policy makers (one and five interviews respectively). The production systems chosen are described below and summarised in Table 5.2.

Many ranchers told me that they were switching to calf production because of a rapid price increase driven by a fall in national calf production. This was caused by

**Table 5.2** The four production systems I investigated, their outputs and their requirements.

Name	Outputs	Supporting production	Imports
Business as usual	Calves and cows	Calves and maize	Nothing
Calf-producer	Calves	Maize	Nothing
Cow-producer	Cows	Calves and maize	Nothing
Calf-maize-importer	Cows	Nothing	Calves and maize

severe droughts in northern Mexico and can be seen at a national level (Fig. A.15). I therefore explored a “Calf-producer” production system to investigate the possibility of TD focusing on calf production.

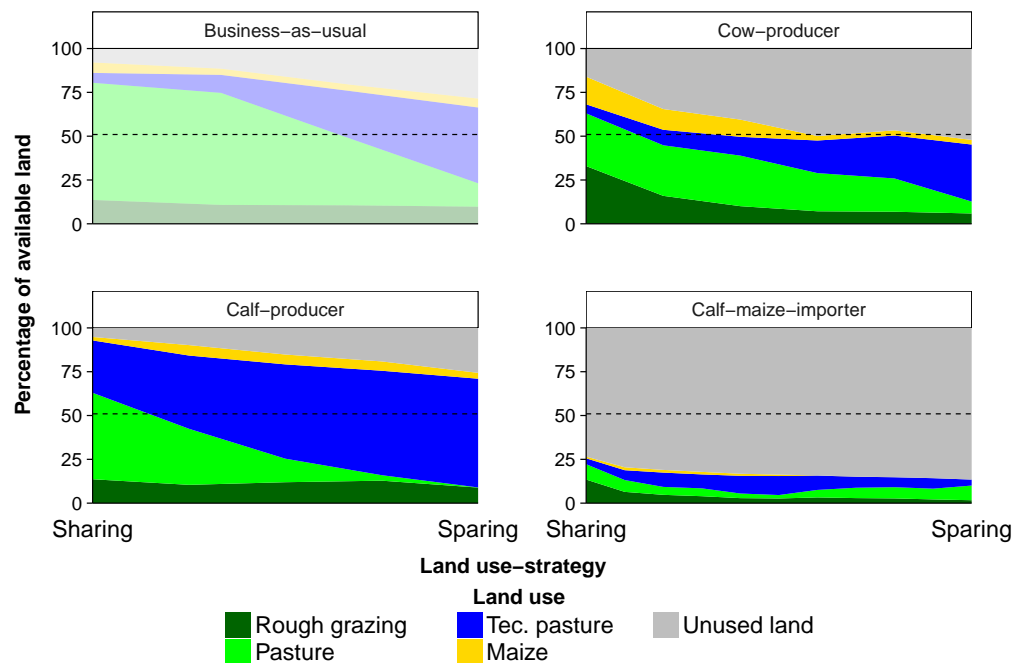
At the same time as market forces are driving increased calf production, local and regional policy makers told me that they were trying to encourage a switch from breeding to finishing ranches, in order to keep a larger portion of the value chain within the region. I used a “Cow-producer” production system to investigate the effects of TD reducing its production of calves for export and a ‘Calf-maize-importer” production system to investigate the effects of importing calves and maize and focusing all production on fattening animals for slaughter.

For each production system I then used the same scenario-building procedure as for the Business-as-usual system (Fig. 5.3), but with some modifications: for Calf-producer I assumed all grazing land and maize production was for breeding ranches, set the cow protein production target to zero and set the maximum production target for calf protein as 170% of the current production of calf and finished cow protein combined. For Cow-producer and Calf-maize-importer I set the calf-protein production target to zero and set the maximum production target for finished cow protein as 170% of the current production of calf and finished cow protein combined. In addition, for Calf-maize-importer I assumed that all grazing land was used for finishing ranches and set site requirements to zero (to model the effect of importing calves and maize).

### 5.7.1 Results: Land use and biodiversity impacts of different production systems

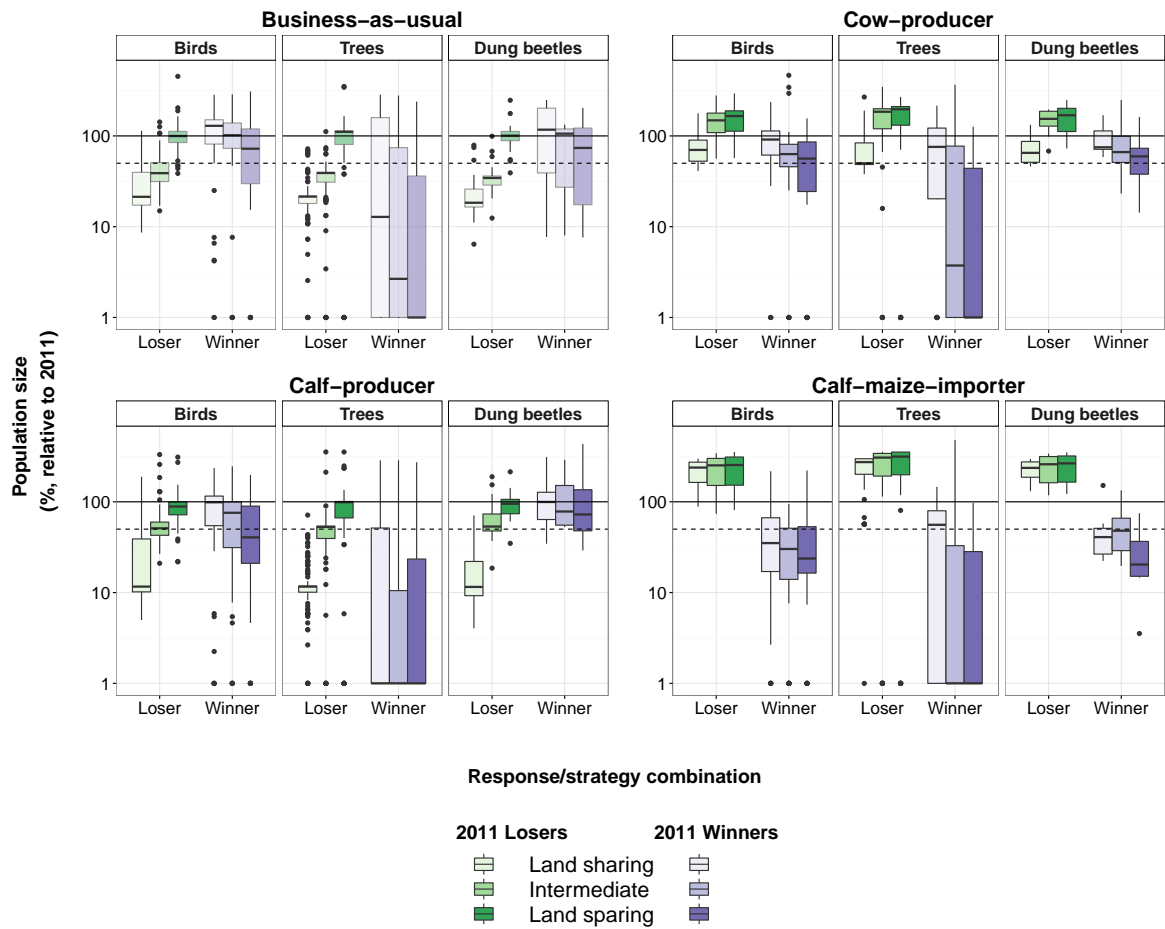
Land-use patterns for the alternative production systems were very similar to Business-as-usual: a smaller area of agricultural land was required as yields increased, and there was a shift towards technified pasture, although Calf-maize-importer used relatively more pasture than the other systems (Fig. 5.9). The major difference between production systems was in the total area required to meet the production target: for a

production target of 130% of current production, Business-as-usual and Calf-producer required over 90% of available land under land sharing compared with 27% for Calf-maize-importer. Cow-producer was intermediate, requiring over 80% of available land with land sharing, but under 50% with land sparing.



**Fig. 5.9** Area of different land uses under different land-use strategies and production systems for a 2030 production target of 130% of current production. Values are percentages of the total area of TD and the black dashed line shows the area currently under pasture, technified pasture and maize (from SAGARPA, 2015). Unused land could in theory be spared for nature conservation.

The biodiversity impacts of Calf-producer were similar to Business-as-usual, reflecting the very similar land use patterns in the two systems: relative to 2011, most species declined by 2030, with far greater population declines under land sharing or intermediate strategies than land sparing. The exceptions to this pattern were, again, bird and dung beetle species that were 2011 winners, which suffered less severe declines under land sharing than land sparing (Fig. 5.10). With the Cow-producer system, however, populations of 2011 losers increased relative to 2011 under land sparing or intermediate strategies. With the Calf-maize-importer system, all land use strategies used far less land than is currently under agriculture, meaning that 2011 loser species increased under all land-use strategies. Species that were winners in 2011 showed similar patterns across production systems.



**Fig. 5.10** Estimated 2030 populations of birds, trees, and dung beetles relative to 2011 under different land-use strategies and production systems, assuming a 2030 production target of 130%. Horizontal lines show the median difference in population size, boxes the 1<sup>st</sup> and 3<sup>rd</sup> quartiles, and vertical lines 1.5 times the interquartile range. For clarity, I have used a logarithmic y-axis, truncated the y-axis at 500% of 2011 population sizes, although several species had larger relative populations.

## 5.8 Discussion

### 5.8.1 Overview of results

Despite the variety of taxa, production targets and production systems I analysed, my results were remarkably consistent: most species were losers under agriculture with populations that would be larger under land sparing than any other strategy. These results are consistent with previous studies (e.g. Phalan et al., 2011b; Hulme et al., 2013; Edwards et al., 2014; Dotta et al., 2015; Edwards et al., 2015; Kamp et al., 2015;

Feniuk, 2016), despite my study region's long history of natural and anthropogenic disturbance and the very different agricultural system I studied.

A higher proportion of trees and dung beetles were losers, compared to birds (Figs. 5.5, 5.6) and a higher proportion did least badly with land sparing. Again these results are consistent with previous studies, which found that birds are relatively resilient to agricultural disturbance compared to other taxa (Phalan et al., 2011b; Dotta et al., 2015; Feniuk, 2016). I discuss possible reasons for this in Chapters 4 and 7.

### 5.8.2 Variations in 2030 population sizes

Species that were losers in 2011 are, almost by definition, forest dependent. They therefore declined relative to pre-human populations under all production systems and land-use strategies, and relative to 2011 for production systems that required a lot of land (i.e. Business-as-usual and Calf-producer). Similarly they did least badly with land sparing because it minimises forest loss, and actually increased relative to 2011 under those production systems that used less land than is currently under production (i.e. Cow-producer and Calf-maize-importer).

Winners in 2011, however, are favoured by agriculture and so most had higher populations in scenarios that had a lot of land under agriculture: land sharing and production systems that used large amounts of land. Trees were the exception, declining under almost all production systems and land-use strategies, often to very low levels. Only 32 species of tree were 2011 winners, however, and only four of these had 10 or more records, so the patterns observed could be due to the idiosyncratic responses of a small number of species.

In most production systems only land sparing had high enough yields to meet the highest production targets, highlighting the importance of limiting growth in human food demand.

### 5.8.3 Differences between production systems and the likelihood of different futures

Patterns of land use were consistent across production systems because the relative yields of land uses remained the same whether producing calf or finished cow protein (see Chapter 3). However, the area of land required did vary, with the biggest difference being between Calf-maize-importer and the other production systems. Calf-maize-importer used less than 30% of the land required by Business-as-usual or Calf-producer,

not because it imported maize (which never occupied more than 16% of available land under any production system or land-use strategy), but because it did not produce any calves: because breeding ranches have lower feed conversion ratio and grazing yields, the amount of calf protein produced is a key determinant of the area required.

Because Calf-maize-importer exported so much of its environmental footprint, natural habitat restoration was possible across large areas, allowing the populations of 2011 loser species to increase relative to 2011 (Fig. 5.10). These biodiversity gains would come at a cost to biodiversity elsewhere, as land outside TD would be converted to agriculture. However, because TD currently produces more calves than finished cows (Fig. 5.1), and the area of maize in the region is increasing (Fig. 1.4), the Calf-maize-importer system would appear the least likely to be adopted in the near future.

More relevant is the contrast between Cow-producer and the other two systems. Again, the relative amounts of calf and finished cow protein produced determined overall impact of the scenarios: at a production target of 130% of current production, Cow-producer used a maximum of 40% of available land for breeding ranches. This compared with 77% and 89% for Business-as-usual and Calf-producer respectively. This reduction spared a large amount of land for natural habitat conservation or restoration, to the point where, under land sparing, Cow-producer could use less land than is currently farmed to reach a production target of 130% of current production (Fig. 5.9).

These land use requirements drove the biodiversity patterns seen across production systems: Calf-producer showed similar patterns to Business-as-usual because it had very similar land use requirements (Figs. 5.9, 5.10). In contrast, 2011 losers increased with Cow-producer under land sparing and intermediate strategies, whilst 2011 winners responded similarly to the other production systems.

The degree to which TD concentrates on either calf or finished cow production will therefore be key in determining the impact of cattle ranching in the region. Recent trends suggest the production of finished cows is likely to increase relative to calves (Fig. 5.1) and this is supported by qualitative, semi-structured interviews I performed with policy makers and union leaders. These actors were keen to keep a higher proportion of the value chain of beef production within Yucatán by increasing in-state slaughtering and processing.

However, this shift is not corroborated by anecdotal evidence from my three field seasons. Many ranchers told me that they were switching to calf production as prices increased rapidly in response to the fall in national calf production caused by severe droughts in northern Mexico. This reduction can be seen at a national level (Fig. A.15),

although my quantitative interviews did not show calf prices increasing faster than finished cow prices (*unpublished interviews*).

How Yucatecan cattle production develops will therefore depend on both initiatives to promote meat production within the state and market forces determining the relative profitability of calves and cows. This in turn will depend heavily on the recovery of cattle production in the north of Mexico. The fate of Yucatecan biodiversity may therefore be determined as much by the climate in northern Mexico over the coming decades as by public policy.

## 5.9 Conclusions

Across all taxa, production targets and production systems, land sparing allowed more species to maintain larger populations than any other land-use strategy. This pattern was strongest for species that were losers in 2011. For probable 2030 production targets, most land-use scenarios resulted in a decline in forest area and a corresponding decline in the populations of most species. Combining land sparing with a shift towards finished cow, rather than calf, production could spare enough land for forest conservation or restoration, but to achieve this will require mechanisms that explicitly link yield increases with habitat protection. I discuss these in Chapter 7. Land-use strategies affect more than just biodiversity, and in Chapter 6 I use the scenarios developed here to investigate the effects of different land-use strategies and production systems on regional carbon stocks.







## CHAPTER 6

### CARBON STOCKS AND AGRICULTURE

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*“We are not an endangered species ourselves yet, but this is not for lack of trying”*

Douglas Adams – *Last Chance to See*

#### 6.1 Introduction

Controlling land-use change has been proposed as a cost effective way to reduce anthropogenic CO<sub>2</sub> emissions and mitigate climate change (e.g. Stern, 2007). Land-use change is the second biggest source of anthropogenic CO<sub>2</sub> emissions after fossil fuel combustion with the majority of the 12–35% of emissions attributable to tropical deforestation and forest degradation (Houghton et al., 2001; Gibbs et al., 2007; van der Werf et al., 2009; Defries and Rosenzweig, 2010). Because tropical land rents tend to be relatively low, several studies have suggested that the opportunity costs of forest conservation or reforestation will be correspondingly low and that deforestation could be greatly reduced at a carbon price as low as US\$5–21 per tonne CO<sub>2</sub> (Stern, 2007; Kindermann et al., 2008).

To understand the feasibility of controlling CO<sub>2</sub> emissions in this way, and to devise land-use strategies that store carbon whilst providing food and other ecosystem services, we need to know how carbon stocks vary across land uses and agricultural yields. The link between carbon stocks and agricultural yield is similar to that between yields and biodiversity: stocks are likely to be highest in natural habitats, and to decline as yields increase and tree cover decreases. As with biodiversity, therefore, we need an analytical framework that explicitly links agricultural yields with carbon stocks, and addresses the issue of leakage by comparing landscapes that produce the same amount of food.

Deforestation in south-east Mexico has been a major source of carbon dioxide emissions, with the region losing perhaps 20% of its total non-soil carbon stock between 1977 and 1992: equivalent to 36% of Mexico's net emissions from land use change over the period, from only 24% of its area (Cairns et al., 2000). There are several published estimates of forest carbon stocks from the region but I found no studies looking at stocks in cattle pastures or across yields.

To fill this data gap I analysed the relationship between live carbon stocks and agricultural yield using density-yield functions. I then used the land use scenarios developed in Chapter 5 to investigate how regional live carbon stocks are likely to vary with different agricultural land-use strategies.

## **6.2 Methods**

### **6.2.1 Estimating live carbon stocks in study sites**

To estimate live carbon stocks in my study sites I combined the above- and belowground estimates obtained from my fieldwork. Because I was unable to sample soil and standing litter crop stocks I assumed that these were constant across sites (see Section 2.4). To investigate the effects of different land-use strategies, I therefore analysed only the live carbon stocks.

### **6.2.2 Variation of live carbon stocks across agricultural yields**

To investigate how live carbon stocks varied with agricultural yields I used the site yields estimated in Chapter 4, based on the land uses in each site and their grazing or maize yields. I used the same maximum-likelihood optimisation procedure as in Chapter 4 to fit two possible carbon density-yield functions. Model (1) is monotonic, whereas Model (2) allows stocks to increase and then decrease:

$$(1) : \quad n/v = \exp(b_0 + b_1 x^\alpha)$$

$$(2) : \quad n/v = \exp(b_0 + b_1 x^\alpha + b_2 x^{2\alpha})$$

where:

$n$  = the estimated live carbon stock for the site (MgC)

$v$  = the total area surveyed in the site (ha)

$x$  = the yield of the square in kilograms of animal protein (in finished cow equivalents) per hectare per year (kg animal protein ha<sup>-1</sup> yr<sup>-1</sup>)

I selected Model (1) for reasons of parsimony, unless Model (2) had a residual deviance more than 3.84 lower (critical  $\chi^2$  value for one degree of freedom at  $p = 0.05$ ).

I set target and permissible yields as in Chapter 4 and calculated the mean regional live carbon stock density in the same way as I calculated mean population densities.

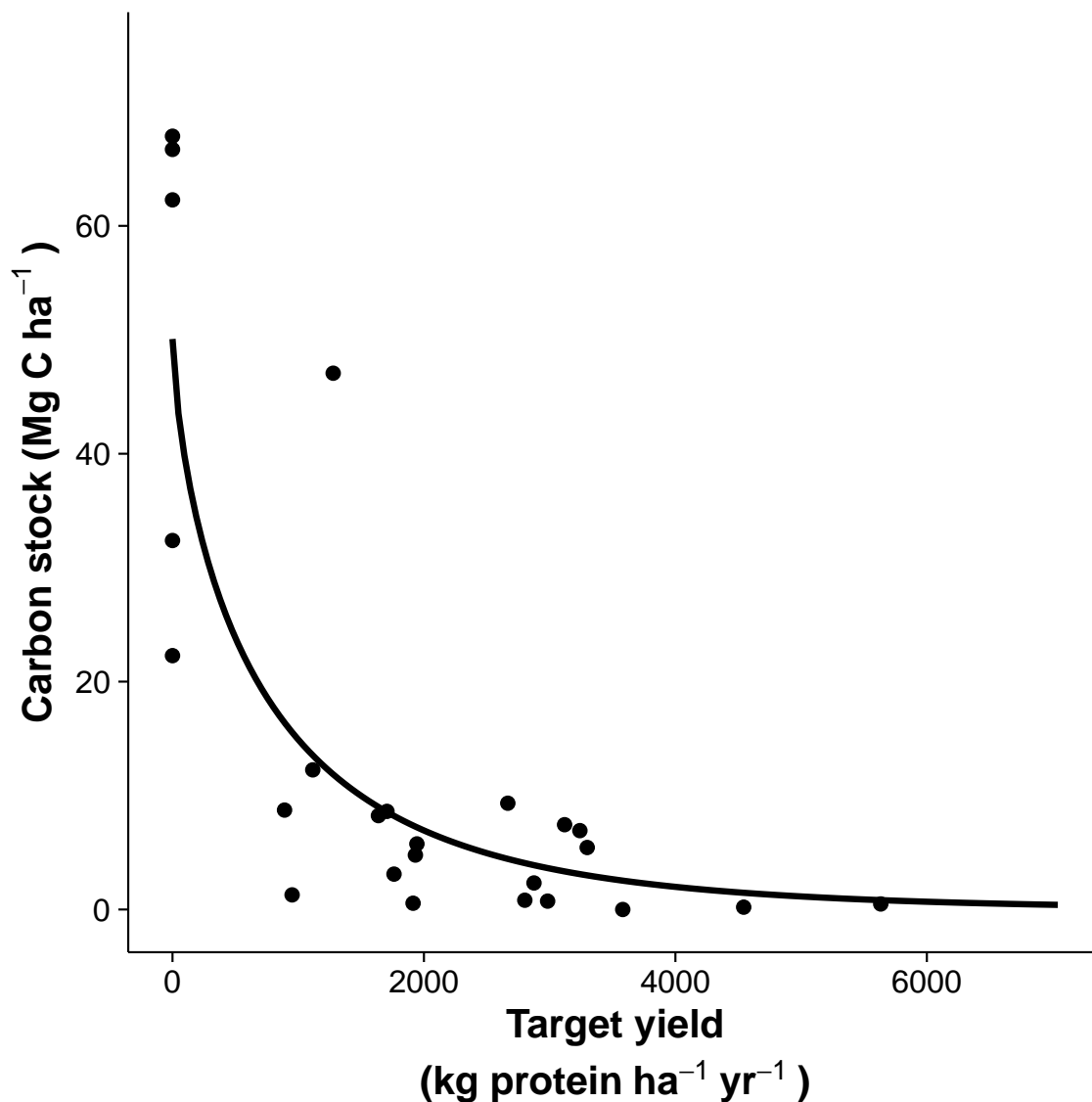
### 6.2.3 Regional live carbon stocks under different land use scenarios

I used live carbon stock estimates for each study site and the land use scenarios built in Chapter 5 to estimate regional live carbon stocks in Tizimín District (TD) with different production targets and land-use strategies, for the four production systems investigated. I multiplied the number of times a site was used in a scenario by its live carbon stock estimate, using the mean live carbon stock estimates for the five baseline sites as the value for natural habitats.

## 6.3 Results

### 6.3.1 Variation of carbon stocks across agricultural yields

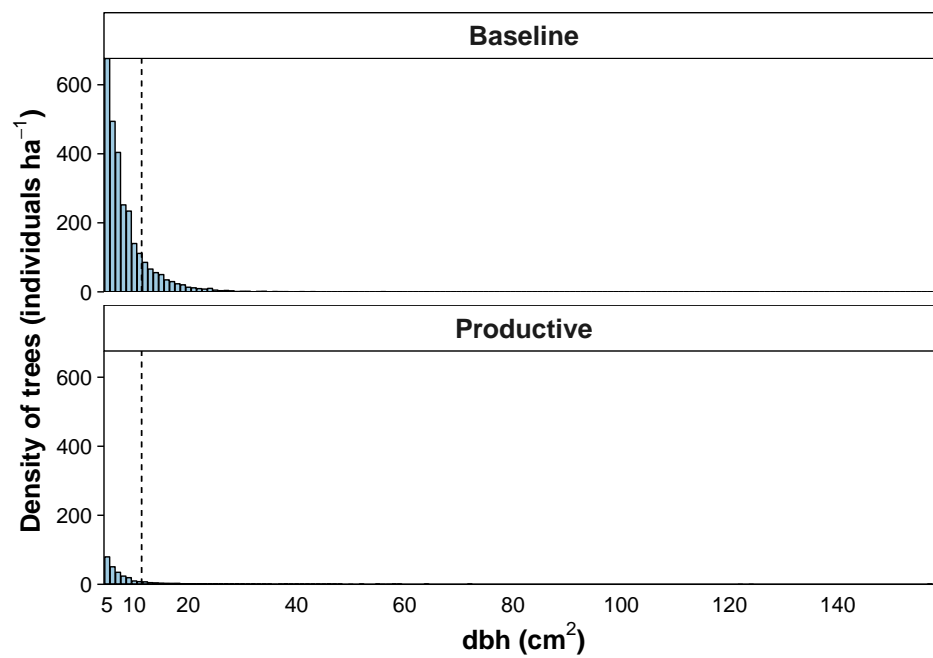
Live carbon stocks declined rapidly with agricultural yields and then levelled off (Fig. 6.1). Baseline sites had more, but not larger trees (Fig. 6.2) and across both baseline and productive sites, small trees contributed a high proportion of live carbon (Fig. 6.3).



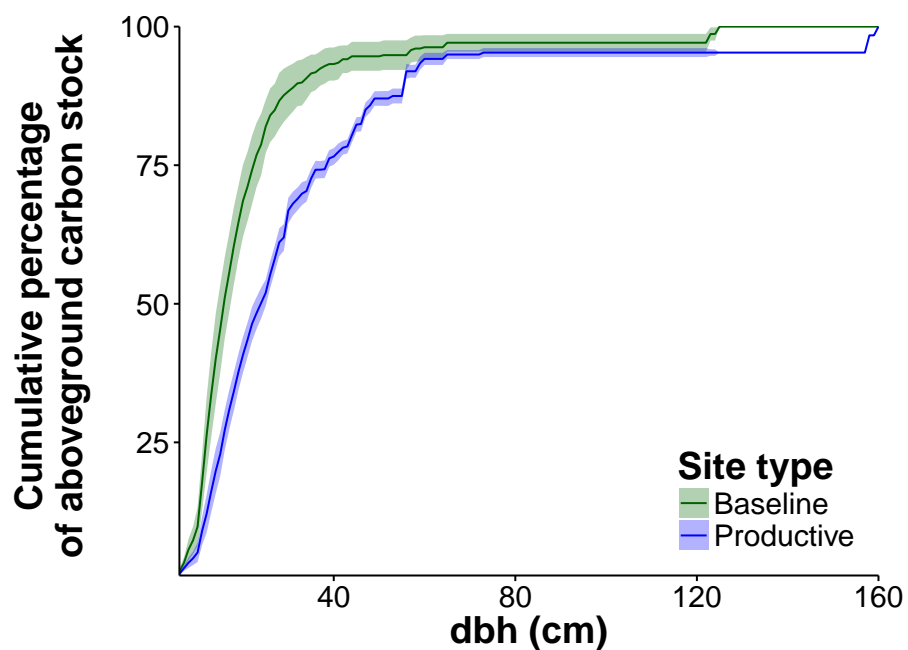
**Fig. 6.1** Density-yield function for live (above- and below-ground) carbon stocks in Yucatecan cattle ranches.

### 6.3.2 Regional carbon stocks under different land use scenarios

All production systems show very similar results: a largely linear decrease in stocks as the production target increases (Fig. 6.4). For the Business-as-usual and Calf-producer production systems, the biggest differences in regional stocks were between land sparing and intermediate strategies (rather than with land sharing) until 110% of



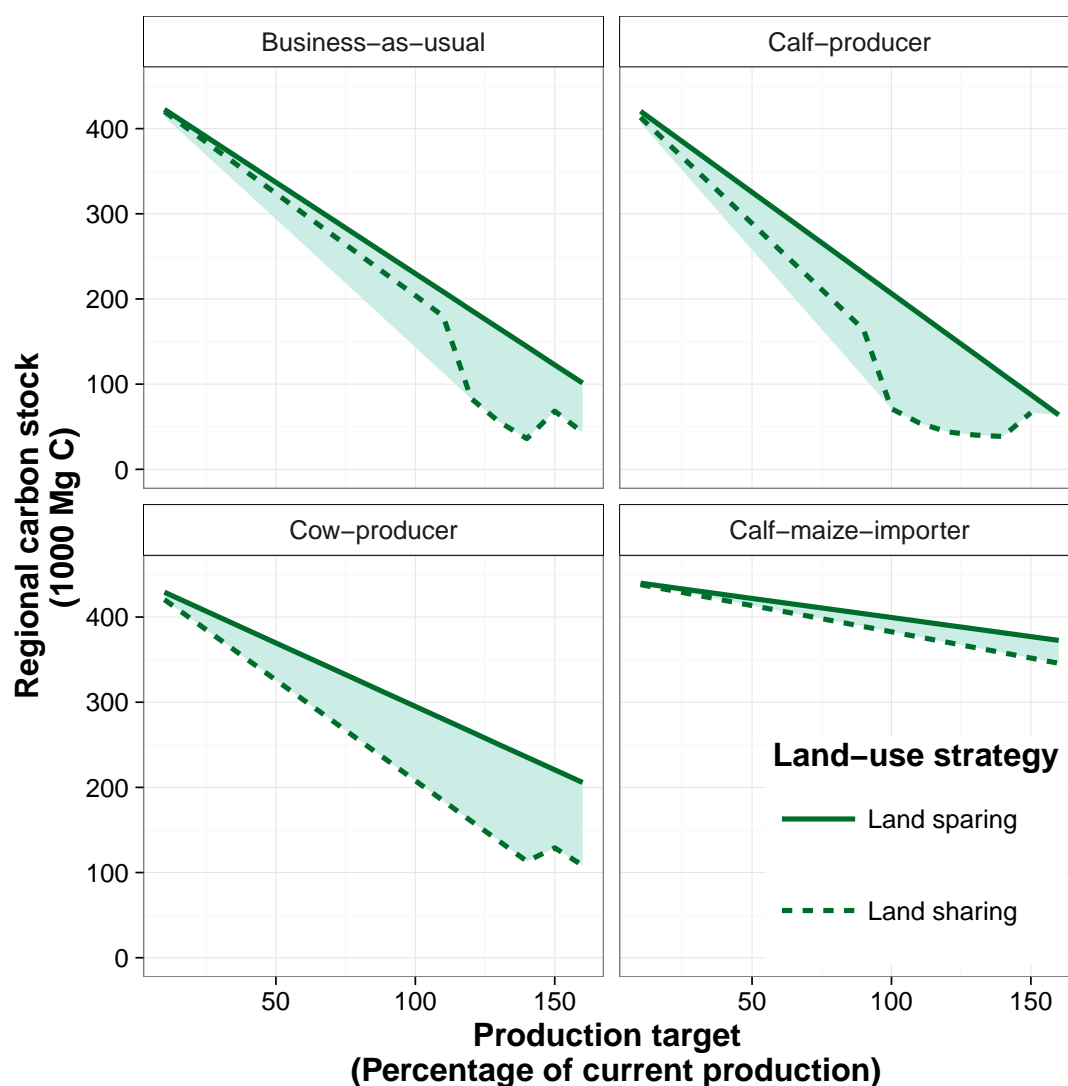
**Fig. 6.2** Size-density distributions for trees in baseline and productive study sites. Dashed lines show the median tree size for each site type.



**Fig. 6.3** Cumulative percentage of aboveground carbon stocks stored in trees of different dbh classes. Lines show the mean values for five baseline and twenty productive sites. Shaded areas show the standard deviation of 10,000 bootstrapped samples of the sites.

current production. After this there was a rapid decline in the carbon stocks under land sharing, whilst stocks under land sparing continued to decrease linearly.

Stocks declined faster with the Business-as-usual and Calf-producer production systems than with Cow-producer and Calf-maize-importer because the former used considerably more land (see Fig. 5.9).



**Fig. 6.4** Estimated regional live carbon stocks for Tizimín District under different production systems and land-use strategies. Shaded areas show stocks under intermediate production strategies. I do not show the highest probable 2030 production target of 170% of current production because it can only be met by a land sparing strategy. In addition, for Calf-producer, only land sparing can meet a production target of 160% of current production.



## 6.4 Discussion

Live carbon stocks change with yield in the same way as loser species that do least badly with land sparing: with highest stocks in baseline sites and a rapid decline as agricultural yields rise above zero. Regional carbon stocks were therefore maximised by land sparing, which maintains the largest coverage of natural habitats. What was more surprising was that, with the Business-as-usual and Calf-producer production systems, land sharing maintained higher carbon stocks than intermediate-yield strategies until production targets were 110% of current production (Fig. 6.4). This was due to land-sharing scenarios making use of a traditional ranch site that was entirely covered in grazed forest (see Section 2.1). This site had a live carbon density of  $47.1 \text{ t ha}^{-1}$ ; far higher than any other productive site (with a maximum of  $12.3 \text{ t ha}^{-1}$ ) and comparable to the mean value for baseline sites ( $50.3 \text{ t ha}^{-1}$ ). Above a production target of 110% of current production however, this site was no longer productive enough to be used in any strategy and so the carbon stocks under land sharing fell rapidly.

My stock estimates were within the range of those found elsewhere in the Yucatán Peninsula (YP, see Section 2.4). I could find no studies looking at carbon stocks in cattle ranches in the region but my results support Gilroy et al. (2014b, 's) findings from cattle-ranching landscapes in Colombia, which found that a land-sparing strategy allowed greater regional carbon storage for a given level of cattle production than land sharing. Global-scale analyses have also suggested that land sparing is likely to result in lower greenhouse gas emissions in the next century than other land-use strategies (e.g. Foley et al., 2011; Tilman et al., 2011), and could even result in net carbon sequestration if coupled with yield increases and diet shifts (Lamb et al., 2016b).

To test the sensitivity of my results to including soil and litter carbon stocks, I repeated the analyses using the lowest and highest published values for these stocks from the YP. I found no qualitative differences in the results (Figs A.16—A.17. These analyses, however, assumed a that carbon and litter stocks remained constant across land uses, which is unlikely to be the case. Many studies have shown how soil organic carbon stocks decrease when forest is converted into cropland (e.g. Murty et al., 2002; Czimczik et al., 2005), but there is much greater uncertainty over how they vary with conversion to pasture (Murty et al., 2002). It is possible that the deep-rooted African grasses used in Yucatecan pastures combined with specific management practices could increase soil carbon stocks (Fisher et al., 1994; Conant et al., 2001; Fujisaki et al., 2015). These practices, such as better grazing management and the use of legumes such as *Leucaena leucocephala* are used in high yielding systems, so it is possible that

a land-sparing approach could actually increase carbon stocks on agricultural land, as well as maintaining larger areas of natural habitat. To investigate this requires either long-term data series or study sites of different ages but matched for other characteristics (e.g. Eaton and Lawrence, 2009).

## 6.5 Conclusions

Carbon stocks declined rapidly with increasing agricultural yield due to a rapid drop in living biomass. For any given production target, therefore, regional carbon stocks were maximised with land sparing. These results are robust to uncertainty over the size of soil and standing litter crop stocks which made up a high percentage of total stocks in all sites. I discuss these results in relation to my biodiversity findings in Chapter 7).





## DISCUSSION

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*“There is one last reason for caring, and I believe that no other is necessary. It is certainly the reason why so many people have devoted their lives to protecting the likes of rhinos, parakeets, kakapos, and dolphins. And it is simply this: the world would be a poorer, darker, lonelier place without them.”*

Mark Cardawine – *Last Chance to See*

In this chapter I review the principal findings from my research in the context of previous studies on the trade-offs between food production and the conservation of biodiversity and ecosystem services. I briefly explore the issue of using a suitable baseline for these studies before considering how the land sparing/land sharing framework can be expanded to address a wider range of issues and to permit more nuanced analyses. Finally I explore how land sparing could operate in practice, both in Yucatán and elsewhere.

### 7.1 Overview of results

My density-yield analyses show that most species of birds, trees and dung beetles in northeast Yucatán require natural habitats to maintain high population densities. This finding is reflected in the results of my scenario building, which found that larger populations of more species could be supported with land sparing than any other strategy. Carbon stocks followed a similar pattern: declining rapidly as natural habitats are converted into agricultural land and being maximised at a regional scale under a land-sparing regime.

My results support previous work on trade-offs between food production and the conservation of biodiversity or ecosystem services (Phalan et al., 2011b; Hulme et al., 2013; Edwards et al., 2014; Gilroy et al., 2014b; Dotta et al., 2015; Edwards et al., 2015; Kamp et al., 2015; Feniuk, 2016). This is somewhat surprising because Yucatán has a long history of both natural and anthropogenic disturbance. Forests in the Yucatán Peninsula (YP) have expanded and contracted with climatic changes (del Socorro Lozano-García, 2007) and the region is regularly subject to hurricanes and tropical storms (Boose et al., 2003; Whigham et al., 2003). Moreover, there have been repeated waves of anthropogenic deforestation: first by the Pre-Classic (1000 BCE – 250 CE) and Classic (250–900 CE) Mayan civilisations; then by 19<sup>th</sup> century *sisal* (*Agave sisalana*) and *henequen* (*Agave fourcroydes*) plantations; and finally by 20<sup>th</sup> century cattle ranching. It might be anticipated that such strong evolutionary and ecological pressure would cause the extinction of many disturbance-sensitive species and so lead to a relatively resilient biota (Balmford, 1996), with a lower proportion of species that do least badly with land sparing and more winners than in other systems. In fact, relative benefits of land sparing are similar to in previous work and whilst I found a slightly higher proportion of winners than in some systems (e.g. birds in South American pampas or Kazakh steppe, Dotta et al., 2015; Kamp et al., 2015) it was lower than in others (e.g. birds in Uttarakhand, Phalan, 2009).

I found variation in how taxa respond to increased agricultural yields: more bird species were winners and fewer were favoured by land sparing than were trees or dung beetles (although most were still losers that did least badly with land sparing). This is in accord with studies in Ghana, India, Brazil and Uruguay and Poland (Phalan et al., 2011b; Dotta, 2013; Feniuk, 2016) and may reflect birds' relative mobility. This suggests it is important to monitor taxa other than birds to understand the full effect of agricultural disturbance.

The similarity of my results to previous studies is also important because I investigated a wider range of cattle ranching systems than previous studies, from rough grazing in forest to irrigated pastures and maize production. It has been proposed that low yield cattle ranching has a high biodiversity value (e.g. Derner et al., 2009), but my analyses show that in the YP these systems do not maintain high enough densities of forest-dependent species to offset the biodiversity cost of the larger area they require.

Importantly, my results are robust to the choice of baseline I used. The accuracy of an all-forest baseline is debatable given that the forest in the YP suffers regular hurricane damage and has expanded and contracted with periodic droughts. Whilst

relative population changes differed when using a 2011 or all-forest baseline, in both cases land sparing allowed more species to maintain larger populations.

My results also support previous analyses of carbon storage under different land-use strategies: Gilroy et al. (2014a) found that carbon storage in low-yield agricultural land is unlikely to offset that lost by increased conversion of natural habitats. Wade et al. (2010) found slightly different results in cocoa plantations in Ghana, with land sharing being preferable at low production targets. However, at targets above current production, land sparing stored more carbon across their study region.

My results are robust to uncertainties in yield estimates, and to the inclusion or exclusion of rare species (as well as choice of baseline), and serve to re-emphasise the importance of natural habitat protection for both biodiversity conservation and the maintenance of carbon stocks. Whilst most species' population densities and carbon stocks continue to decline as yields increase, it is the initial change from natural habitats that is the most damaging. This strongly suggests that natural habitat protection is therefore more important for maintaining biodiversity and carbon stocks than is attempting to conserve species on agricultural land, if on-farm conservation measures incur a yield penalty.

## 7.2 Expanding the assessment of land sparing

My analyses are not spatially explicit and do not account for edge effects or metapopulation dynamics, or include demographic information. Previous land sparing studies have been criticised for failing to account for the effect of different matrices on the probability of population persistence in patches of natural habitat (e.g. Perfecto and Vandermeer, 2008). However, the strength of my results, and the negative relationship between matrix suitability (which is likely to decline with increasing yields) and patch size (which can increase with increasing yields), means that they are unlikely to change qualitatively with the incorporation of metapopulation dynamics into my analyses. Investigating the trade-off between matrix suitability and patch size directly, through spatially explicit population modelling would, however, allow increased confidence in my results. Such an approach has been adopted for investigating edge effects and Lamb et al. (2016a) found that in Ghana these reduce the effectiveness of a land-sparing strategy for conserving birds, but that land sharing was still preferable only with a combination of large edge effects and a very high degree of fragmentation in the landscape. Including demographic information, for example on reproductive rates, could also alter my results. However, unless natural habitats act as a sink habitat,

and low yield farmland as a source, this is again very unlikely to alter my overall conclusions.

The land use strategy that does the least environmental damage will depend on more than just biodiversity and carbon storage. Soil protection, nutrient cycling, water quality regulation and zoonotic disease dynamics are all important considerations that affect the sustainability of production, human welfare and the wider environment. Research is needed into how these other ecosystem services interact with land use and agricultural yield, so as to identify underlying trade-offs and synergies.

Non-agricultural land uses can also have important environmental impacts. Whilst studies of logging in Borneo (Edwards et al., 2014) and urban development in Japan (Soga et al., 2014) suggest that equivalents of land sparing allow more biodiversity to survive, further research is needed in other land uses, other regions and with other ecosystem services.

Research is also needed into the social aspects of agriculture. Different land uses will employ different land tenure systems, support different levels of employment, and can lead to different levels of social equity, food security and well-being. How these factors vary with agricultural yield is very poorly understood, but robust comparisons of different systems are needed to understand the impacts of land-use decisions on individuals and society (e.g. Fischer et al., 2014). More diverse yield metrics would also add to these analyses: protein production, energy yield and profit generation do not capture everything that society or farmers expect from agriculture (Sutherland, 2004). Understanding how aesthetic, cultural and even religious values vary with land uses could help us not only to uncover the ends of land use planning, but also the means to get there.

### 7.3 Sustainable livestock production in practice

Adopting land sparing as a strategy to reduce harm to biodiversity and carbon stocks is necessary but not sufficient to achieve sustainable livestock production. Demand reduction, achieving sustainable high yields and ensuring that high yields are linked to land sparing are all key considerations.



### 7.3.1 Supply and demand

Under most land-use scenarios, achieving probable 2030 production targets will result in forest loss in the YP, so limiting growth in the demand for beef will be necessary to prevent the consequent loss of biodiversity and carbon stocks.

Such demand reduction would have enormous benefits outside the region. Ruminant meat is extremely inefficient to produce and so has huge environmental impacts: contributing far more greenhouse gas emissions and using more water, land and reactive nitrogen per gram of protein produced, per calorie, or per serving than any other foodstuff (Eshel et al., 2014; Tilman and Clark, 2014). As rates of meat consumption are well correlated with wealth (Tilman and Clark, 2014) they are likely to continue to increase. Decoupling this relationship will therefore be crucial if sustainable food production, biodiversity conservation and climate change mitigation are to be achieved over the next century.

### 7.3.2 Sustainable high yields

Not all mechanisms to increase yields are equal in their environmental impacts. Excessive irrigation can deplete aquifers and lead to salinisation but better irrigation practices can greatly reduce water requirements. I also found that mechanised, but non-irrigated pasture has similar yields to irrigated pasture, potentially allowing high yield agriculture to increase in coverage without proportionally increasing environmental impacts. High livestock yields also require high stocking densities which can increase groundwater pollution (e.g. Tamminga, 2003; Pokhrel et al., 2012), and this relationship may be more difficult to decouple. Groundwater is the only water source in the YP but it is unclear how different land uses influence local and regional pollution (Hernández-Terrones et al., 2010). Understanding how stocking densities relate to pollutant levels, and how these can be minimised is an important area of research for delivering sustainable high yields in the YP.

Several of my study sites contained areas of intensive silvopastoral systems (ISPS): technified pastures with high density *Leucaena leucocephala* plantings. I was not able to investigate these independently, because they did not cover a large enough proportion of my study sites, but they have been promoted in the tropics as a more sustainable way of increasing yields compared to monoculture pastures through the provision of extra protein and shade, and also of increasing animal welfare, on-farm biodiversity and ecosystem services, and reducing ruminant methane production (Broom et al., 2013; Cuartas-Cardona et al., 2014 but see Beauchemin et al., 2008). Again, because I was

not able to analyse ISPS within my study sites separately, I cannot conclude whether they were beneficial for biodiversity or carbon storage. However, if they increase yields above those of technified pastures they potentially allow more land to be spared and so could have benefits for biodiversity and carbon storage irrespective of their on-farm impacts.

### 7.3.3 Achieving land sparing

A land sparing strategy will only benefit biodiversity and carbon storage if the yield increases achieved by converting pastures to technified pastures or ISPS are linked to a reduction in forest clearance. There is some evidence that yield increases can passively spare land if increased production can satisfy demand, thereby making it less profitable to clear land (Ewers et al., 2009). However, if increased yields lower commodity prices and therefore increase demand, or increase the profitability of farming and hence the opportunity cost of conserving or restoring natural habitats, they could lead to agricultural expansion (Angelsen, 2010). Which scenario occurs may depend on whether land is used to produce staples or higher value goods. Demand for staples such as wheat, for direct human consumption, is relatively inelastic. However, more discretionary, higher-value goods, such as beef, have a more elastic demand. Lower costs and increased incomes can therefore drive demand for land (Kaimowitz and Angelsen, 2008). Mechanisms for actively linking yield increases and habitat conservation are therefore important to realising the benefits of land sparing, particularly for systems producing higher-value goods.

Phalan et al. (2016) identified four broad mechanisms of active land sparing: land-use zoning; the spatially strategic deployment of technology, infrastructure, or agronomic knowledge; economic instruments; and standards and certification. Land-use zoning is already used in Mexico, and the YP has four biosphere reserves (although three are largely coastal, IUCN and UNEP-WCMC, 2016). Enforcing forest protection around remaining forest patches, combined with the strategic deployment of resources to allow ranchers to convert existing pastures to technified pastures or ISPS could allow productivity increases without increasing the area under production. The National Commission for the Knowledge and Use of Biodiversity (CONABIO) have recently established a project to the west of Tizimín District to increase the use of ISPS with the explicit aim to reduce pasture expansion (CONABIO interviewee, *pers. comm.*). It is too early to identify results from the project but my interviewees in CONABIO explained that ranchers and union leaders were very receptive to the idea and they

were hopeful that they would soon be able assess the project's initial success in meeting its objectives.

Some Mexican farming subsidies also have environmental conditions attached. The Programme for the Sustainable Production and Management of Livestock and Beekeeping (PROGAN, a programme to support smallholder ranchers), stipulates that producers must plant or protect 30 trees for every animal unit for which they receive support (SAGARPA, 2007). PROGAN is currently being updated and several officials involved in its development told me that they were hoping to increase the ambition of the environmental aspect. Unfortunately enforcement of these regulations is dependent on a small number of officials, but the structures are in place to link farmer support with forest protection or restoration.

In addition, an estimated 431,850 ha of agricultural land have some form of environmental certification in Mexico (Tayleur et al., *in prep.*), suggesting that there may be the potential for a 'land sparing' certification. However, this represents less than 3% of all cropland and only 0.3% of pastures (with only Organic certification contributing significantly to pasture certification). The potential of certification for Mexican cattle production to deliver land sparing will therefore depend not only on the development of an explicit land sparing certification scheme, but also on consumer demand for certified beef products.

Even with these mechanisms in place, land sparing faces challenges. Decisions about agricultural land use are complex, and, in addition to meeting consumer demand, cattle ranching may expand because it is seen as a safe investment or is encouraged by subsidies, because it allows producers to claim more land or gain social status, or because of 'social spillover' whereby new producers take up cattle ranching because others are making money from it (Van Ausdal, 2009; Busch and Vance, 2011). Similarly, policy formation is complex and policy makers will respond to multiple influences, of which a desire to protect the environment is only one (Adams and Sandbrook, 2013).

It is important to note, however, that any other land-use strategy will also suffer from these same problems: increasing on-farm biodiversity by keeping yields artificially low is likely to require significant payments, and the poor performances of agri-environment schemes within the Europe's Common Agricultural Policy shows that even then, such payments are not guaranteed to achieve their objectives (e.g. Kleijn et al., 2001). Moreover, the lower yields mean that, because more farmland is needed to meet demand, regional forest loss is likely to increase and habitat conversion could even be displaced to other regions. In addition, reducing yields is potentially socially regressive and likely to be unpopular with producers. In contrast, my interviewees across local

and national policy makers, cattle unions, ranchers themselves and environmental groups were all broadly supportive of the yield increases necessary for land sparing (*unpublished interviews*).

## 7.4 Conclusions

My research suggests that any land-use strategy in Tizimín District is likely to result in forest loss and considerable environmental harm if current consumption trends continue. Land sparing does less damage than any other land use strategy; in practice this means converting pastures to technified pastures or ISPSs and combining these changes with strict habitat protection or restoration. This strategy is largely aligned with the interests of most stakeholders. However, to safeguard the region's biodiversity and reduce its contribution to climate change, active land-sparing mechanisms must be designed and implemented and efforts made to limit the growing demand for beef.

## REFERENCES

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- Adams, W. M. and Sandbrook, C. (2013). Conservation, evidence and policy. *Oryx*, 47(03):329–335.
- Allen, M. F. and Rincon, E. (2003). The changing global environment and the Lowland Maya: past patterns and current dynamics. In Gómez-Pompa, A., Allen, M. F., Fedick, S., and Jiménez-Osornio, J. J., editors, *The Lowland Maya area: three millennia at the human-wildland interface*, pages 13–29. The Hawthorn Press, Binghamton, NY, New York.
- Angelsen, A. (2010). Policies for reduced deforestation and their impact on agricultural production. *Proceedings of the National Academy of Sciences of the United States of America*, 107(46):19639–19644.
- Animal Feed Resources Information System (2014). <http://www.feedipedia.org/>, last checked December 2014.
- Baba, K. (2007). *Analysis of Productivity, Nutritional Constraints and Management Options in Beef Cattle Systems of Eastern Yucatan, Mexico: a Case Study of Cow-Calf Productivity in the Herds of Tizimin, Yucatan*. PhD thesis, Cornell University.
- Balmford, A. (1996). Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution*, 11(5):193–196.
- Balmford, A., Bruner, A., Cooper, P., and Costanza, R. (2002). Economic reasons for conserving wild nature. *Science*.
- Balmford, A., Green, R., and Phalan, B. (2012). What conservationists need to know about farming. *Proceedings of the Royal Society B: Biological Sciences*, 279:2714–2724.
- Baraloto, C., Molto, Q., Rabaud, S., Hérault, B., Valencia, R., Blanc, L., Fine, P. V., and Thompson, J. (2012). Rapid Simultaneous Estimation of Aboveground Biomass and Tree Diversity Across Neotropical Forests: A Comparison of Field Inventory Methods. *Biotropica*, 45(3):288–298.
- Barlow, J., Gardner, T. A., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. I. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A. M., Miranda-Santos, R., Nunes-Gutjahr, A. L., Overal, W. L., Parry, L., Peters,

- S. L., Ribeiro-Junior, M. A., da Silva, M. N. F., da Silva Motta, C., and Peres, C. A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*, 104(47):18555–18560.
- Barragán, F., Moreno, C. E., Escobar, F., Halffter, G., and Navarrete, D. (2011). Negative impacts of human land use on dung beetle functional diversity. *PLOS One*, 6(3):e17976.
- Basto-Estrella, G. and Rodríguez-Vivas, R. I. (2012). Escarabajos estercoleros (Coleoptera: Scarabaeidae: Scarabaeinae) de ranchos ganaderos de Yucatán, México. *Revista Mexicana de Biodiversidad*, 83:380–386.
- Basto-Estrella, G. S., Rodríguez-Vivas, R. I., Delfin-González, H., and Reyes Novelo, E. (2013). Dung beetle (Coleoptera: Scarabaeinae) diversity and seasonality in response to use of macrocyclic lactones at cattle ranches in the mexican neotropics. *Insect Conservation and Diversity*, 7(1):73–81.
- Beauchemin, K. A., Kreuzer, M., O'mara, F., and Mcallister, T. A. (2008). Nutritional management for enteric methane abatement: a review. *Australian Journal of Experimental Agriculture*, 48:21–27.
- Benjamin, T. J., Montañez, P. I., Jaménez, J. J. M., and Gillespie, A. R. (2001). Carbon, water and nutrient flux in Maya homegardens in the Yucatan peninsula of Mexico. *Agroforestry Systems*, 53(2):103–111.
- Benton, T., Vickery, J., and Wilson, J. (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, 18(4):182–188.
- Berger, J. (1990). Persistence of Different-sized Populations: An Empirical Assessment of Rapid Extinctions in Bighorn Sheep. *Conservation biology*, 4(1):91–98.
- Bernstein, A. S. and Ludwig, D. S. (2008). The Importance of Biodiversity to Medicine. *JAMA*, 300(19):2297–2299.
- Bhagwat, S., Willis, K., and Birks, H. (2008). Agroforestry: a refuge for tropical biodiversity? *Trends in Ecology and Evolution*, 23(5):261–267.
- Signal, E. and McCracken, D. (1996). Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology*, 33:413–424.
- BirdLife International (2015). World Bird Database, [www.birdlife.org/datazone/](http://www.birdlife.org/datazone/) checked several times 2013–2015.
- Bivand, R., Keitt, T., and Rowlingson, B. (2015). *rgdal: Bindings for the Geospatial Data Abstraction Library*.
- Blake, J. G. (1992). Temporal variation in point counts of birds in a lowland wet forest in Costa Rica. *The Condor*, 94(1):265–275.
- Bonilla-Moheno, M. (2012). Damage and recovery of forest structure and composition after two subsequent hurricanes in the Yucatan Peninsula. *Carribean Journal of Sciences*, 46(2–3):1–9.

- Boose, E., Foster, D., Barker Plotkin, A., and Hall, B. (2003). Geographical and histriocal variation in hurricanes across the yucatan peninsular. In Gomez-Pompa, A., Allen, M. F., Fedick, S. L., and Jimenez-Osornio, editors, *The Lowland Maya Area: Three Millennia at the Human-Wildland Interface*, pages 495–516. The Hawthorn Press, Binghamton, NY.
- Boyle, B., Hopkins, N., Lu, Z., Garay, J. A. R., Mozzherin, D., Rees, T., Matasci, N., Narro, M. L., Piel, W. H., Mckay, S. J., et al. (2013). The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC bioinformatics*, 14:16.
- Briske, D. D., Derner, J. D., Brown, J. R., Fuhlendorf, S. D., Teague, W. R., Havstad, K. M., Gillen, R. L., Ash, A. J., and Willms, W. D. (2007). Rotational grazing on rangelands: reconciliation of perception and experimental evidence. *Rangeland Ecology & Management*, 61(1):3–17.
- Brooks, T., Pimm, S., and Oyugi, J. (1999). Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology*, 13(5):1140–1150.
- Broom, D. M., Galindo, F. A., and Murgueitio, E. (2013). Sustainable, efficient livestock production with high biodiversity and good welfare for animals. *Proceedings of the Royal Society B: Biological Sciences*, 280(1771):1–9.
- Brown, S. and Lugo, A. E. (1982). The Storage and Production of Organic Matter in Tropical Forests and Their Role in the Global Carbon Cycle. *Biotropica*, 14(3):161.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., and Laake, J. L. (2005). *Distance sampling*. John Wiley & Sons, Ltd, Chichester, West Sussex.
- Burlingame, B. and Sandro, D. (2012). *Sustainable Diets and Biodiversity. Directions and Solutions for Policy, Research and Action*. Nutrition and Consumer Protection Division, FAO.
- Burnham, K. P. and Anderson, D. R. (2002). *Model selection and multimodel inference*. Springer Verlag, New York. Springer Verlag, 2nd edition.
- Busch, C. and Vance, C. (2011). The Diffusion of Cattle Ranching and Deforestation—Prospects for a Hollow Frontier in Mexico’s Yucatán. Technical Report 242, Rheinisch-Westfälisches Institut für Wirtschaftsforschung (RWI), Bochum, Germany.
- Cairns, M., Haggerty, P., Alvarez, R., De Jong, B., and Olmsted, I. (2000). Tropical Mexico’s recent land-use change: A region’s contribution to the global carbon cycle. *Ecological Applications*, 10(5):1426–1441.
- Cairns, M., Olmsted, I., Granados, J., and Argaez, J. (2003). Composition and aboveground tree biomass of a dry semi-evergreen forest on Mexico’s Yucatan Peninsula. *Forest Ecology and Management*, 186(1–3):125–132.
- Cairns, M. A., Brown, S., Helmer, E. H., and Baumgardner, G. A. (1997). Root biomass allocation in the world’s upland forests. *Oecologia*, 111(1):1–11.

- Ceddia, M. G., Bardsley, N. O., Gomez-y Paloma, S., and Sedlacek, S. (2014). Governance, agricultural intensification, and land sparing in tropical South America. *Proceedings of the National Academy of Sciences of the United States of America*, 111(20):7242–7247.
- Cepeda-González, M. F., Escalona-Segura, G., Montero-Muñoz, J., Mendez-Gonzalez, M. E., Pozo-de la Tijera, C., and Hernandez-Betancourt, S. (2011). Composición de especies de aves en potreros de matrices de origen antropogénico y mixto en la Reserva de la Biosfera Ría Lagartos, Yucatán, México. *Brenesia*, 75–76:37–48.
- Chamberlain, D. E., Fuller, R. J., Bunce, R. G. H., Duckworth, J. C., and Shrubbs, M. (2000). Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, 37(5):771–788.
- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martínez-Yrízar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Péliissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G., and Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20(10):3177–3190.
- CICY Herbarium (2014). <http://www.cicy.mx/Sitios/flora%20digital/index.php>, checked several times 2013–2015.
- Clough, Y., Barkmann, J., Juhrendt, J., Kessler, M., Wanger, T. C., Anshary, A., Buchori, D., Cicuzza, D., Darras, K., and Putra, D. D. (2011). Combining high biodiversity with high yields in tropical agroforests. *Proceedings of the National Academy of Sciences of the United States of America*, 108(20):8311–8316.
- CONABIO (1995). Instituto Nacional de investigaciones Forestales y Agropecuarias (INIFAP) – Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO). *Edafología*.
- CONABIO (2015). [www.conabio.gob.mx/informacion/gis/](http://www.conabio.gob.mx/informacion/gis/) checked several times 2013–2015.
- Conant, R. T., Paustian, K., and Elliott, E. T. (2001). Grassland Management and Conversion Into Grassland: Effects on Soil Carbon. *Ecological Applications*, 11(2):343–355.
- Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., and Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, 26:152–158.
- Crawley, M. J. (2005). *Statistics: an introduction using R*. John Wiley & Sons, Ltd, Chichester, West Sussex.



- Cuartas-Cardona, C. A., Naranjo-Ramírez, J. F., Tarazona-Morales, A. M., Murgueitio-Restrepo, E., Chará-Orozco, J. D., Ku-Vera, J., Solorio-Sánchez, F. J., Flores-Estrada, M. X., Solorio-Sánchez, B., and Barahona-Rosales, R. (2014). Contribución de los sistemas silvopastoriles intensivos al desempeño animal y a la adaptación y mitigación al cambio climático. *Revista Colombiana de Ciencias Pecuarias*, 27(2):76–94.
- Czimczik, C. I., Mund, M., Schulze, E.-D., and Wirth, C. (2005). Effects of reforestation, deforestation, and afforestation on carbon storage in soils. *SEB experimental biology series*, 319-330.
- Dagand, A. B. K. and Nair, P. K. R. (2003). Silvopastoral research and adoption in Central America: recent findings and recommendations for future directions. *Agroforestry Systems*, 59:149–155.
- Daily, G., Polasky, S., and Goldstein, J. (2009). Ecosystem services in decision making: time to deliver. *Frontiers in Ecology and the Environment*.
- DeFries, R., Fanzo, J., Remans, R., Palm, C., Wood, S., and Anderman, T. L. (2015). Metrics for land-scarce agriculture. *Science*, 349(6245):238–240.
- Defries, R. and Rosenzweig, C. (2010). Toward a whole-landscape approach for sustainable land use in the tropics. *Proceedings of the National Academy of Sciences of the United States of America*, 107(46):19627–19632.
- del Socorro Lozano-García, M. (2007). Tracing the effects of the Little Ice Age in the tropical lowlands of eastern Mesoamerica. *Proceedings of the National Academy of Sciences of the United States of America*, 104(41):16200–16203.
- Derner, J. D., Lauenroth, W. K., Stapp, P., and Augustine, D. J. (2009). Livestock as ecosystem engineers for grassland bird habitat in the Western Great Plains of North America. *Rangeland Ecology & Management*, 62(2):111–118.
- Diamond, J. M. (1972). Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest pacific islands. *Proceedings of the National Academy of Sciences of the United States of America*, 69(11):3199–3203.
- Dirzo, R. and Raven, P. H. (2003). Global State of Biodiversity and Loss. *Annual Review of Environment and Resources*, 28(1):137–167.
- Donald, P. F., Green, R. E., and Heath, M. F. (2001). Agricultural intensification and the collapse of Europe’s farmland bird populations. *Proceedings of the Royal Society B: Biological Sciences*, 268:25–29.
- Dotta, G. (2013). *Agricultural production and biodiversity conservation in the grasslands of Brazil and Uruguay*. PhD thesis, University of Cambridge.
- Dotta, G., Phalan, B., Silva, T. W., Green, R., and Balmford, A. (2015). Assessing strategies to reconcile agriculture and bird conservation in the temperate grasslands of South America. *Conservation Biology*, 00(0):1–10.

- Eaton, J. M. and Lawrence, D. (2009). Loss of carbon sequestration potential after several decades of shifting cultivation in the Southern Yucatan. *Forest Ecology and Management*, 258(6):949–958.
- Edwards, D. P., Gilroy, J. J., Thomas, G. H., Uribe, C. A. M., and Haugaasen, T. (2015). Land-sparing agriculture best protects avian phylogenetic diversity. *Current biology*, 25(18):2384–2391.
- Edwards, D. P., Gilroy, J. J., and Woodcock, P. (2014). Land-sharing versus land-sparing logging: reconciling timber extraction with biodiversity conservation. *Global Change Biology*, 20:183–191.
- Edwards, D. P., Hodgson, J. A., Hamer, K. C., Mitchell, S. L., Ahmad, A. H., Cornell, S. J., and Wilcove, D. S. (2010). Wildlife-friendly oil palm plantations fail to protect biodiversity effectively. *Conservation Letters*, 3(4):236–242.
- Erwin, T. (1982). Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin*, 36(1):75–76.
- Eshel, G., Shepon, A., Makov, T., and Milo, R. (2014). Land, irrigation water, greenhouse gas, and reactive nitrogen burdens of meat, eggs, and dairy production in the United States. *Proceedings of the National Academy of Sciences of the United States of America*, 111(33):11996–12001.
- Estrada, A., Coates-Estrada, R., and Dadda, A. A. (1998). Dung and Carrion Beetles in Tropical Rain Forest Fragments and Agricultural Habitats at Los Tuxtlas, Mexico. *Journal of Ecology*, 14(5):577–593.
- Ewers, R. M., Scharlemann, J., Balmford, A., and Green, R. (2009). Do increases in agricultural yield spare land for nature? *Global Change Biology*, 15:1716–1726.
- FAO (1972). *Technical conversion factors for agricultural commodities*. Food and Agriculture Organisation, Rome.
- FAO (2015). FAOStat, <http://faostat3.fao.org/home/E>, accessed March 2015.
- Feniuk, C. (2016). *Reconciling food production and biodiversity conservation in Europe*. PhD thesis, University of Cambridge.
- Fischer, J., Abson, D. J., Butsic, V., Chappell, M. J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H. G., and von Wehrden, H. (2014). Land sparing versus land sharing: moving forward. *Conservation Letters*, 7(3):149–157.
- Fisher, M. J., Rao, I. M., Ayarza, M. A., Lascano, C. E., Sanz, J. I., Thomas, R. J., and Vera, R. R. (1994). Carbon storage by introduced deep-rooted grasses in the South American savannas. *Nature*, 371(6494):236–238.
- Foley, J., DeFries, R., Asner, G., Barford, C., Bonan, G., Carpenter, S., Chapin, F., Coe, M., Daily, G., Gibbs, H., Helkowski, J., Holloway, T., Howard, E., Kucharik, C., Monfreda, C., Patz, J., Prentice, I., Ramankutty, N., and Snyder, P. (2005). Global Consequences of Land Use. *Science*, 309(5734):570–574.

- Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K., West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockstrom, J., Sheehan, J., Siebert, S., Tilman, D., and Zaks, D. P. M. (2011). Solutions for a cultivated planet. *Nature*, 478(7369):337–342.
- Fowler, C. and Hodgkin, T. (2004). Plant Genetic Resources for Food and Agriculture: Assessing Global Availability. *Annual Review of Environment and Resources*, 29(1):143–179.
- Frampton, G. K. and Dorne, J. L. (2007). The effects on terrestrial invertebrates of reducing pesticide inputs in arable crop edges: a meta-analysis. *Journal of Applied Ecology*, 44:362–373.
- Fujisaki, K., Perrin, A.-S., Desjardins, T., Bernoux, M., Balbino, L. C., and Brossard, M. (2015). From forest to cropland and pasture systems: a critical review of soil organic carbon stocks changes in Amazonia. *Global Change Biology*, 21(7):2773–2786.
- Gabriel, D., Sait, S. M., Hodgson, J. A., Schmutz, U., Kunin, W. E., and Benton, T. G. (2010). Scale matters: the impact of organic farming on biodiversity at different spatial scales. *Ecology Letters*, 13(7):858–869.
- Garcia, C. A., Bhagwat, S., Ghazoul, J., and Nath, C. D. (2010). Biodiversity conservation in agricultural landscapes: challenges and opportunities of coffee agroforests in the Western Ghats, India. *Conservation Biology*, 24(2):479–488.
- Gardner, T. A., Barlow, J., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. I. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A. M., Miranda-Santos, R., Overal, W. L., Parry, L., Peters, S. L., Ribeiro-Junior, M. A., da Silva, M. N. F., da Silva Motta, C., and Peres, C. A. (2008). The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters*, 11(2):139–150.
- Gardner, T. A., Hernandez, M. I. M., Barlow, J., and Peres, C. A. (2007). Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *Journal of Applied Ecology*, 45(3):883–893.
- Gibbs, H. K., Brown, S., Niles, J. O., and Foley, J. A. (2007). Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environmental Research Letters*, 2(4):045023.
- Gilroy, J. J., Edwards, F. A., Medina Uribe, C. A., Haugaasen, T., and Edwards, D. P. (2014a). Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. *Journal of Applied Ecology*, 51:1337–1346.
- Gilroy, J. J., Woodcock, P., Edwards, F. A., Wheeler, C., Medina Uribe, C. A., Haugaasen, T., and Edwards, D. P. (2014b). Optimizing carbon storage and biodiversity protection in tropical agricultural landscapes. *Global Change Biology*, 20(7):2162–2172.

- Giraldo, C., Escobar, F., Chará, J., and Calle, Z. (2010). The adoption of silvopastoral systems promotes the recovery of ecological processes regulated by dung beetles in the Colombian Andes. *Insect Conservation and Diversity*, 4(2):115–122.
- Gómez-Pompa, A. and Kaus, A. (1999). From pre-Hispanic to future conservation alternatives: lessons from Mexico. *Proceedings of the National Academy of Sciences of the United States of America*, 96(11):5982–5986.
- Gonzalez-Iturbe, J., Olmsted, I., and Tun-Dzul, F. (2002). Tropical dry forest recovery after long term Henequen (sisal, *Agave fourcroydes* Lem.) plantation in northern Yucatan, Mexico. *Forest Ecology and Management*, 167(1–3):67–82.
- Goodman, R. C., Phillips, O. L., and del Castillo Torres, D. (2013). Amazon palm biomass and allometry. *Forest Ecology and Management*, 310:994–1004.
- Google Inc. (2015). Google Earth (Version 7.1).
- Gotelli, N. and Colwell, R. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4:379–391.
- Green, R., Cornell, S., Scharlemann, J., and Balmford, A. (2005). Farming and the fate of wild nature. *Science*, 307:550–555.
- Gustavsson, J., Cedeberg, C., and Sonesson, U. (2011). *Global food losses and food waste—Extent, causes and prevention*. FAO, Rome, Italy.
- Halffter, G. and Arellano, L. (2002). Response of dung beetle diversity to human-induced changes in a tropical landscape. *Biotropica*, 34(1):144–154.
- Halffter, G., Favila, M. E., and Halffter, V. (1992). A comparative study of the structure of the scarab guild in Mexican tropical rain forests and derived ecosystems. *Folia Entomológica Mexicana*, 84:131–156.
- Halffter, G. and Halffter, V. (2009). Why and where coprophagous beetles (Coleoptera: Scarabaeinae) eat seeds, fruits or vegetable detritus. *Boletín de la Sociedad Entomológica Aragonesa*, 45:1–22.
- Halffter, G. and Matthews, E. G. (1966). The natural history of dung beetles of the subfamily scarabaeinae. *Folia Entomologica Mexicana*, 12-14:1–312.
- Hanski, I. and Cambefort, Y. (1991). *Dung Beetle Ecology*. Princeton University Press, New Jersey.
- Haug, G. H., Günther, D., Peterson, L. C., Sigman, D. M., Hughen, K. A., and Aeschlimann, B. (2003). Climate and the collapse of Maya civilization. *Science*, 299(5613):1731–1735.
- Hernández-Stefanoni, J. L., Dupuy, J. M., and Johnson, K. D. (2014). Improving species diversity and biomass estimates of tropical dry forests using airborne LiDAR. *Remote Sensing*, 6:4741–4763.

- Hernández-Terrones, L., Rebolledo-Vieyra, M., Merino-Ibarra, M., Soto, M., Le-Cossec, A., and Monroy-Ríos, E. (2010). Groundwater Pollution in a Karstic Region (NE Yucatan): Baseline Nutrient Content and Flux to Coastal Ecosystems. *Water, Air, & Soil Pollution*, 218(1-4):517–528.
- Hijmans, R. J. (2015). *raster: Geographic Data Analysis and Modeling*.
- Hodell, D. A., Curtis, J. H., and Brenner, M. (1995). Possible role of climate in the collapse of Classic Maya civilization. *Nature*, 375(6530):391–394.
- Hole, D., Perkins, A., Wilson, J., and Alexander, I. (2005). Does organic farming benefit biodiversity? *Biological Conservation*, 122:113–130.
- Horgan, F. G. (2007). Dung beetles in pasture landscapes of Central America: proliferation of synanthropic species and decline of forest specialists. *Biodiversity and Conservation*, 16(7):2149–2165.
- Houghton, R. A., Hackler, J. L., and Cushman, R. M. (2001). Carbon flux to the atmosphere from land-use changes: 1850 to 1990. ORNL/CDIAC-131, NDP-050/R1. Carbon Dioxide Information Analysis Center, U.S. Department of Energy, Oak Ridge National Laboratory, Oak Ridge, Tennessee, U.S.A.
- Howell, S. N. G. and Webb, S. (1995). *A guide to the birds of Mexico and Northern Central America*. Oxford University Press, Oxford, UK.
- Hulme, M. F., Vickery, J. A., Green, R. E., Phalan, B., Chamberlain, D. E., Pomeroy, D. E., Nalwanga, D., Mushabe, D., Katebaka, R., Bolwig, S., and Atkinson, P. W. (2013). Conserving the birds of Uganda’s banana-coffee arc: land sparing and land sharing compared. *PLOS One*, 8(2):e54597.
- INEGI (2015). [www.inegi.org.mx/](http://www.inegi.org.mx/) checked several times 2013–2015.
- IUCN (2015). *The IUCN Red List of Threatened Species. Version 2015-4*.
- IUCN and UNEP-WCMC (2016). *The World Database on Protected Areas (WDPA), March 2016, [www.protectedplanet.net](http://www.protectedplanet.net)*. Cambridge, UK: UNEP-WCMC.
- Jankielsohn, A., Scholtz, C. H., and Louw, S. V. (2001). Effect of habitat transformation on dung beetle assemblages - A comparison between a South African nature reserve and neighboring farms. *Environmental entomology*, 30(3):474–483.
- Kaimowitz, D. and Angelsen, A. (2008). Will livestock intensification help save latin america’s tropical forests? *Journal of Sustainable Forestry*, 27(1-2):6–24.
- Kamp, J., Urazaliev, R., Balmford, A., Donald, P. F., Green, R. E., Lamb, A. J., and Phalan, B. (2015). Agricultural development and the conservation of avian biodiversity on the Eurasian steppes: a comparison of land-sparing and land-sharing approaches. *Journal of Applied Ecology*, 52(6):1578–1587.
- Karp, D. S., Mendenhall, C. D., Sandí, R. F., Chaumont, N., Ehrlich, P. R., Hadly, E. A., and Daily, G. C. (2013). Forest bolsters bird abundance, pest control and coffee yield. *Ecology Letters*, 16(11):1339–1347.

- Kindermann, G., Obersteiner, M., Sohngen, B., Sathaye, J., Andrasko, K., Rametsteiner, E., Schlamadinger, B., Wunder, S., and Beach, R. (2008). Global cost estimates of reducing carbon emissions through avoided deforestation. *Proceedings of the National Academy of Sciences of the United States of America*, 105(30):10302–10307.
- King, D. A., Davies, S. J., Tan, S., and Noor, N. S. M. (2006). The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology*, 94(3):670–680.
- Kleijn, D., Berendse, F., Smit, R., and Gilissen, N. (2001). Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature*, 413(6857):723–725.
- Laake, J., Borchers, D., Thomas, L., Miller, D., and Bishop, J. (2015). *mrds: Mark-Recapture Distance Sampling*. R package version 2.1.14.
- Lamb, A., Balmford, A., Green, R. E., and Phalan, B. (2016a). To what extent could edge effects and habitat fragmentation diminish the potential benefits of land sparing? *Biological Conservation*, 195:264–271.
- Lamb, A., Green, R., Bateman, I., Broadmeadow, M., Bruce, T., Burney, J., Carey, P., Chadwick, D., Crane, E., Field, R., Goulding, K., Griffiths, H., Hastings, A., Kasoar, T., Kindred, D., Phalan, B., Pickett, J., Smith, P., Wall, E., zu Ermgassen, E. K. H. J., and Balmford, A. (2016b). The potential for land sparing to offset greenhouse gas emissions from agriculture. *Nature Climate Change*, Advance online publication.
- Larsen, T. and Forsyth, A. (2005). Trap Spacing and Transect Design for Dung Beetle Biodiversity Studies. *Biotropica*, 37(2):322–325.
- Larsen, T. H., Lopera, A., and Forsyth, A. (2006). Extreme trophic and habitat specialization by peruvian dung beetles (coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin*, 60(4):315–324.
- Larsen, T. H., Lopera, A., and Forsyth, A. (2008). Understanding trait-dependent community disassembly: Dung beetles, density functions, and forest fragmentation. *Conservation Biology*, 22(5):1288–1298.
- Larsen, T. H., Williams, N. M., and Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters*, 8(5):538–547.
- Lawrence, D. and Foster, D. (2002). Changes in forest biomass, litter dynamics and soils following shifting cultivation in southern Mexico: An overview. *Interciencia*, 27(8):400–408.
- Liu, K. (1999). Millennial-scale variability in catastrophic hurricane landfalls along the Gulf of Mexico coast. *23rd Conference on Hurricanes and Tropical Meteorology. American Meteorological Society, Dallas, TX*.

- Liu, K.-b. and Fearn, M. L. (2000). Reconstruction of Prehistoric Landfall Frequencies of Catastrophic Hurricanes in Northwestern Florida from Lake Sediment Records. *Quaternary Research*, 54(2):238–245.
- Lynch, J. (1995). Effects of point count duration, time-of-day, and aural stimuli on detectability of migratory and resident bird species in Quintana Roo, Mexico. *USDA Forest Service General Technical Report*, 149:1–6.
- MacDicken, K. G. (1998). *A Guide to Monitoring Carbon Storage in Forestry and Agroforestry Projects*. Winrock International Institute for Agricultural Development, Forest Carbon Monitoring Program.
- Mannetje, L. (1997). Potential and prospects of legume-based pastures in the tropics. *Tropical Grasslands*, 31:81–94.
- Marsh, C. J., Louzada, J., Beiroz, W., and Ewers, R. M. (2013). Optimising bait for pitfall trapping of Amazonian dung beetles (Coleoptera: Scarabaeinae). *PLOS One*, 8(8):e73147.
- Mastrangelo, M. E. and Gavin, M. C. (2012). Trade-offs between cattle production and bird conservation in an agricultural frontier of the Gran Chaco of Argentina. *Conservation biology : the journal of the Society for Conservation Biology*, 26(6):1040–1051.
- Mastrangelo, M. E. and Gavin, M. C. (2014). Impacts of agricultural intensification on avian richness at multiple scales in Dry Chaco forests. *Biological Conservation*, 179:63–71.
- Moore, J. E., Brant, M. H., Kunkle, W. E., and Hopkins, D. I. (1999). Effects of supplementation on voluntary forage intake, diet digestibility, and animal performance. *Journal of Animal Science*, 77 Suppl 2:122–135.
- Morin, X. and Chuine, I. (2006). Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology Letters*, 9:185–195.
- Murty, D., Kirschbaum, M., and Mcmurtrie, R. E. (2002). Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. *Global Change Biology*, 8:105–123.
- Natural England, Forestry Commission, and The European Agricultural Fund for Rural Development: Europe investing in rural areas (2015). Countryside Stewardship: Options and Supplements.
- Navarrete, D. and Halffter, G. (2008). Dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) diversity in continuous forest, forest fragments and cattle pastures in a landscape of Chiapas, Mexico: the effects of anthropogenic changes. *Biodiversity and Conservation*, 17(12):2869–2898.
- Nichols, E., Gardner, T. A., Peres, C. A., Spector, S., and The Scarabaeinae Research Network (2009). Co-declining mammals and dung beetles: an impending ecological cascade. *Oikos*, 118(4):481–487.

- Nichols, E., Larsen, T., Spector, S., and Davis, A. L. (2007). Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. *Biological Conservation*, 137:1–19.
- Nichols, E., Spector, S., Louzada, J., and Larsen, T. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, 141:1461–1474.
- Nichols, E., Uriarte, M., Bunker, D. E., Favila, M. E., Slade, E. M., Vulinec, K., Larsen, T., Vaz-de Mello, F. Z., Louzada, J., Naeem, S., and Spector, S. H. (2013). Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. *Ecology*, 94(1):180–189.
- Nichols, E. S. and Gardner, T. A. (2011). Dung beetles as a candidate study taxon in applied biodiversity conservation research. In Simmons, L. W. and Ridsdill-Smith, T. J., editors, *Ecology and Evolution of Dung Beetles*, pages 267–291. Blackwell Publishing Ltd.
- Norton, B. E. (1998). The application of grazing management to increase sustainable livestock production. *Animal production in Australia*, 22:15–26.
- Ødegaard, F. (2000). How many species of arthropods? Erwin’s estimate revised. *Biological Journal of the Linnean Society*, 71:583–597.
- Oksanen, J. (2013). Vegan: ecological diversity. *R Vignette*, pages 1–11.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O’Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., and Wagner, H. (2015). *vegan: Community Ecology Package*. R package version 2.3-3, <https://CRAN.R-project.org/package=vegan>.
- Olson, D., Dinerstein, E., and Wikramanayake, E. (2001). Terrestrial ecoregions of the world: a new map of life on earth. *BioScience*, 51(11):993–938.
- Orihuela-Belmonte, D. E., de Jong, B. H. J., Mendoza-Vega, J., Van der Wal, J., Paz-Pellat, F., Soto-Pinto, L., and Flamenco-Sandoval, A. (2013). Carbon stocks and accumulation rates in tropical secondary forests at the scale of community, landscape and forest type. *Agriculture Ecosystems & Environment*, 171:72–84.
- Pal, J. S. and Eltahir, E. A. B. (2015). Future temperature in southwest Asia projected to exceed a threshold for human adaptability. *Nature Climate Change*, 6(2):197–200.
- Patz, J. A., Campbell-Lendrum, D., Holloway, T., and Foley, J. A. (2005). Impact of regional climate change on human health. *Nature*, 438(7066):310–317.
- Pelletier, N., Pirog, R., and Rasmussen, R. (2010). Comparative life cycle environmental impacts of three beef production strategies in the Upper Midwestern United States. *Agricultural systems*, 103(6):380–389.
- Perfecto, I. and Vandermeer, J. (2008). Biodiversity conservation in tropical agroecosystems. *Annals of the New York Academy of Sciences*, 1134(1):173–200.



- Perfecto, I., Vandermeer, J., Mas, A., and Pinto, L. (2005). Biodiversity, yield, and shade coffee certification. *Ecological Economics*, 54:435–446.
- Phalan, B. (2009). *Land use, food production, and the future of tropical forest species in Ghana*. PhD thesis, University of Cambridge.
- Phalan, B., Balmford, A., Green, R. E., and Scharlemann, J. P. W. (2011a). Minimising the harm to biodiversity of producing more food globally. *Food Policy*, 36:S62–S71.
- Phalan, B., Green, R. E., Dicks, L. V., Dotta, G., Feniuk, C., Lamb, A., Strassburg, B. B. N., Williams, D. R., Ermgassen, E. K. H. J. z., and Balmford, A. (2016). How can higher-yield farming help to spare nature? *Science*, 351(6272):450–451.
- Phalan, B., Onial, M., Balmford, A., and Green, R. E. (2011b). Reconciling food production and biodiversity conservation: Land sharing and land sparing compared. *Science*, 333(6047):1289–1291.
- Pokhrel, Y. N., Hanasaki, N., Yeh, P. J.-F., Yamada, T. J., Kanae, S., and Oki, T. (2012). Model estimates of sea-level change due to anthropogenic impacts on terrestrial water storage. *Nature Geoscience*, 5(6):1–4.
- QGIS Development Team (2015). QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>.
- R Core Team (2015). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rabinowitz, D., Cairns, S., and Dillon, T. (1986). Seven forms of rarity and their frequency in the flora of the British Isles. In Soulé, M., editor, *Conservation Biology: The Science of Scarcity and Diversity*, pages 182–204. Sinauer, Sunderland, MA.
- Ramankutty, N., Evan, A. T., Monfreda, C., and Foley, J. A. (2008). Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles*, 22(1):GB1003.
- Ramankutty, N. and Foley, J. A. (1998). Characterizing patterns of global land use: An analysis of global croplands data. *Global Biogeochemical Cycles*, 12(4):667–685.
- Rappole, J. H. and McDonald, M. V. (1994). Cause and effect in population declines of migratory birds. *The Auk*, 111(3):652–660.
- Read, L. and Lawrence, D. (2003). Recovery of biomass following shifting cultivation in dry tropical forests of the Yucatan. *Ecological Applications*, 13(1):85–97.
- Reid, R., Galvin, K., and Kruska, R. S. (2008). Global Significance of Extensive Grazing Lands and Pastoral Societies: An Introduction. In Galvin, K. A., Reid, R. S., Jr, R. H. B., and Hobbs, N. T., editors, *Fragmentation in Semi-Arid and Arid Landscapes*, pages 1–24. Springer, Netherlands.
- Reyes Novelo, E., Delfin-González, H., and Angel Morón, M. (2007). Copro-necrophagous beetle (Coleoptera: Scarabaeidae) diversity in an agroecosystem in Yucatan, Mexico. *Revista de Biología Tropical*, 55(1):83–99.

- Roa-Fuentes, L. L., Hidalgo, C., Etchevers, J. D., and Campo, J. (2013). The effects of precipitation regime on soil carbon pools on the Yucatan Peninsula. *Journal of Tropical Ecology*, 29(05):463–466.
- Rost, S., Gerten, D., Bondeau, A., Lucht, W., Rohwer, J., and Schaphoff, S. (2008). Agricultural green and blue water consumption and its influence on the global water system. *Water Resources Research*, 44(9):1–17.
- SAGARPA (2007). Lineamientos específicos del componente Producción Pecuaria Sostenible Ordenamiento Ganadero y Apícola (PROGAN) del Programa de Uso Sustentable de Recursos Naturales para la Producción Primaria de las Reglas de Operación de los Programas de al Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación.
- SAGARPA (2015). Servicio de Información Agroalimentaria y Pesquera, <http://infosiap.siap.gob.mx/> checked several times 2013-2015.
- Schlenker, W. and Roberts, M. J. (2009). Nonlinear temperature effects indicate severe damages to U.S. crop yields under climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 106(37):15594–15598.
- Shiklomanov, I. A. (2000). Appraisal and assessment of world water resources. *Water International*, 25(1):11–32.
- Smith, A., Ortiz, J., and Robertson, R. (2001). Distribution patterns of migrant and resident birds in successional forests of the Yucatan peninsula, Mexico. *Biotropica*, 33(1):153–170.
- Smith, H. G., Dänhardt, J., Lindström, Å., and Rundlöf, M. (2010). Consequences of organic farming and landscape heterogeneity for species richness and abundance of farmland birds. *Oecologia*, 162(4):1071–1079.
- Soga, M., Yamaura, Y., Koike, S., and Gaston, K. J. (2014). Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation? *Journal of Applied Ecology*, 51(5):1378–1386.
- Steffan-Dewenter, I., Kessler, M., and Barkmann, J. (2007). Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *Proceedings of the National Academy of Sciences of the United States of America*, 104(12):4973–4978.
- Stern, N. (2007). *The economics of climate change: the Stern Review*. Cambridge University Press.
- Sutherland, I. A. and Leathwick, D. M. (2011). Anthelmintic resistance in nematode parasites of cattle: a global issue? *Trends in parasitology*, 27(4):176–181.
- Sutherland, W. (2004). A blueprint for the countryside. *Ibis*, 146(Suppl. 2):230–238.
- Tamminga, S. (2003). Pollution due to nutrient losses and its control in European animal production. *Livestock Production Science*, 84:101–111.

- Tayleur, C. M., Balmford, A., Buchanan, G., Butchart, S., D, D., H, G. R., Milder, J. M., Thomas, D., Sanderson, F., Vickery, J. A., and Phalan, B. (In prep.). Global coverage of agricultural sustainability standards, and their role in conserving biodiversity.
- Tetetla-Rangel, E. and Durán, G. R. (2012). Distribución espacial de la riqueza de especies leñosas raras de la Península de Yucatán y su relación con las áreas naturales protegidas. *Tropical Conservation Science*, 3:320–339.
- The Royal Society (2009). *Reaping the benefits: Science and the sustainable intensification of global agriculture*. The Royal Society, London.
- Tilman, D., Balzer, C., Hill, J., and Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences of the United States of America*, 108(50):20260–20264.
- Tilman, D. and Clark, M. (2014). Global diets link environmental sustainability and human health. *Nature*, 515(7528):518–522.
- Tilman, D., Isbell, F., and Cowles, J. M. (2014). Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45(1):471–493.
- Tilman, D., May, R. M., Lehman, C. L., and Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature*, 371:65–66.
- Tomlinson, I. (2013). Doubling food production to feed the 9 billion: A critical perspective on a key discourse of food security in the UK. *Journal of Rural Studies*, 29:81–90.
- Traylor, Jr, M. A. (1979). Two sibling species of *Tyrannus* (Tyrannidae). *The Auk*, 96(2):221–233.
- UCR Herbarium (2014). University of California Riverside, <http://www.herbarium.ucr.edu/UCR.html>, last accessed May 2014.
- Urquiza-Haas, T., Dolman, P. M., and Peres, C. A. (2007). Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: Effects of forest disturbance. *Forest Ecology and Management*, 247(1–3):80–90.
- USFDA (2015). United States Food and Drug Administration Nutritional Database, <http://ndb.nal.usda.gov/> last accessed June 2014.
- Van Ausdal, S. (2009). Pasture, profit, and power: An environmental history of cattle ranching in Colombia, 1850–1950. *Geoforum*, 40(5):707–719.
- van der Werf, G. R., Morton, D. C., DeFries, R. S., Olivier, J. G. J., Kasibhatla, P. S., Jackson, R. B., Collatz, G. J., and Randerson, J. T. (2009). CO<sub>2</sub> emissions from forest loss. *Nature Geoscience*, 2(11):737–738.
- Van Vliet, N., Mertz, O., Heinimann, A., and Langanke, T. (2012). Trends, drivers and impacts of changes in swidden cultivation in tropical forest-agriculture frontiers: a global assessment. *Global environmental . . . .*

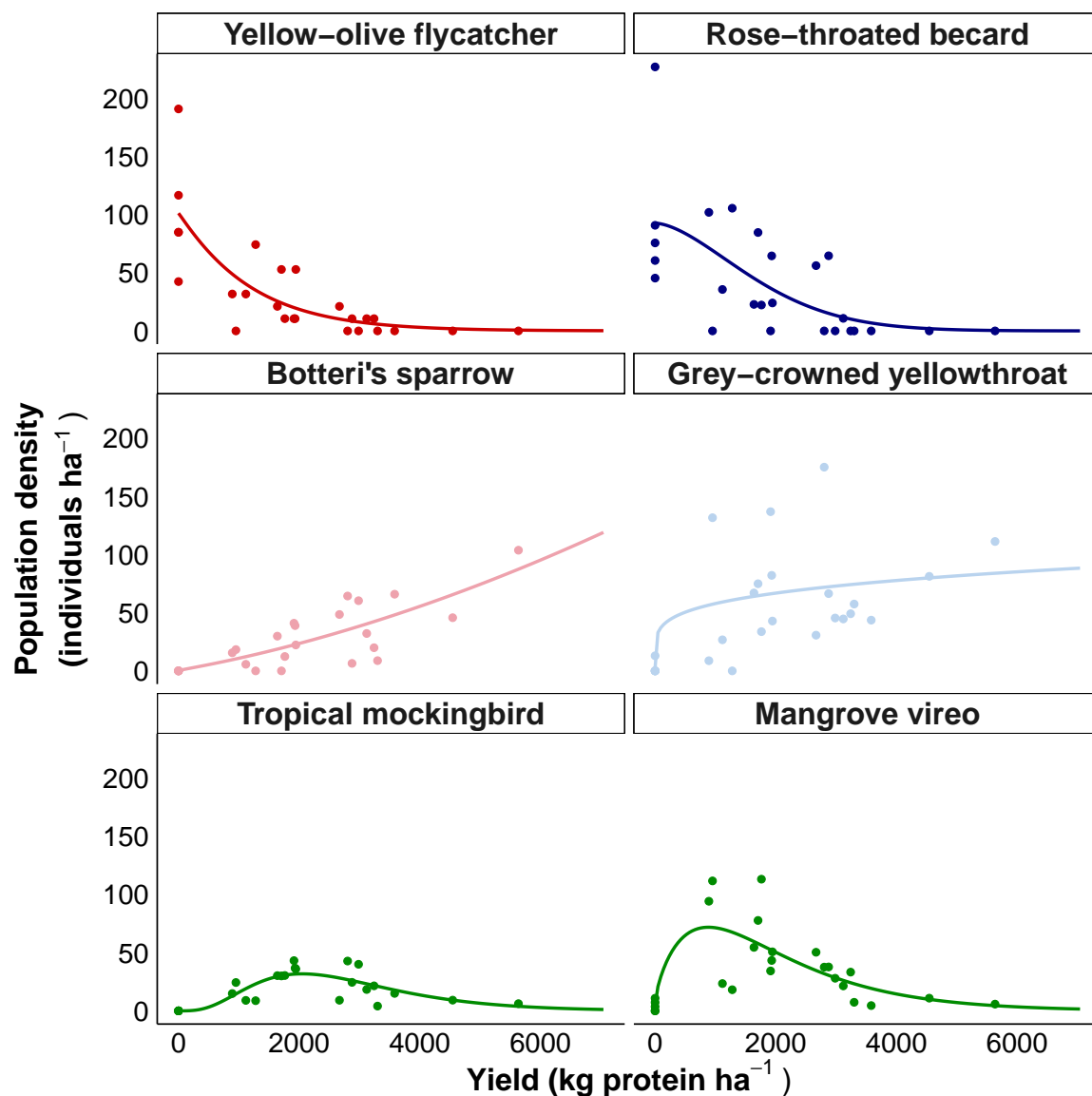
- Vargas, R., Allen, M. F., and Allen, E. B. (2007). Biomass and carbon accumulation in a fire chronosequence of a seasonally dry tropical forest. *Global Change Biology*, 14:109–124.
- Vázquez-Domínguez, E. and Arita, H. (2010). The Yucatan Peninsula: biogeographical history 65 million years in the making. *Ecography*, 33(2):212–219.
- Verhulst, J., Báldi, A., and Kleijn, D. (2004). Relationship between land-use intensity and species richness and abundance of birds in Hungary. *Agriculture, Ecosystem and Environment*, 104:465–473.
- Wade, A., Asase, A., Hadley, P., Mason, J., Ofori-Frimpong, K., Preece, D., Spring, N., and Norris, K. (2010). Management strategies for maximizing carbon storage and tree species diversity in cocoa-growing landscapes. *Agriculture Ecosystems & Environment*, 138:324–334.
- Weisbach, C., Tiessen, H., and Jimenez-Osornio, J. J. (2002). Soil fertility during shifting cultivation in the tropical Karst soils of Yucatan. *Agronomie*, 22(3):253–263.
- Whigham, D., Olmsted, I., Cano, E., and Curtis, A. B. (2003). Impacts of hurricanes on the forests of quintana roo, yucatán peninsula, mexico. In Fedick, S., Allen, A., Jimenez-Osornio, J., and Gómez-Pompa, A., editors, *The Lowland Maya Area: Three Millennia at the Human-Wildland Interface*, pages 193–213. The Hawthorn Press, Binghamton, NY.
- Whitman, A., III, J., and Brokaw, N. (1997). A comparison of two bird survey techniques used in a subtropical forest. *The Condor*, 99(4):955–965.
- Wise, T. A. (2012). The Cost to Mexico of U.S. Corn Ethanol Expansion . *Global Development and Environmental Institute Working Paper No. 12-01*.
- World Bank (2008). *Colombia, Costa Rica, and Nicaragua - Integrated Silvopastoral Approaches to Ecosystem Management Project*. Technical report, Washington, DC.
- Wright, H. L., Lake, I. R., and Dolman, P. M. (2011). Agriculture-a key element for conservation in the developing world. *Conservation Letters*, 5(1):11–19.
- Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S., Miller, R., Swenson, N., Wiemann, M., and Chave, J. (2009). Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.234> last checked May 2014.
- Zidar, C. and Elisens, W. (2009). Sacred giants: Depiction of bombacoideae on maya ceramics in mexico, guatemala, and belize. *Economic Botany*, 63:119–129.

## APPENDIX A

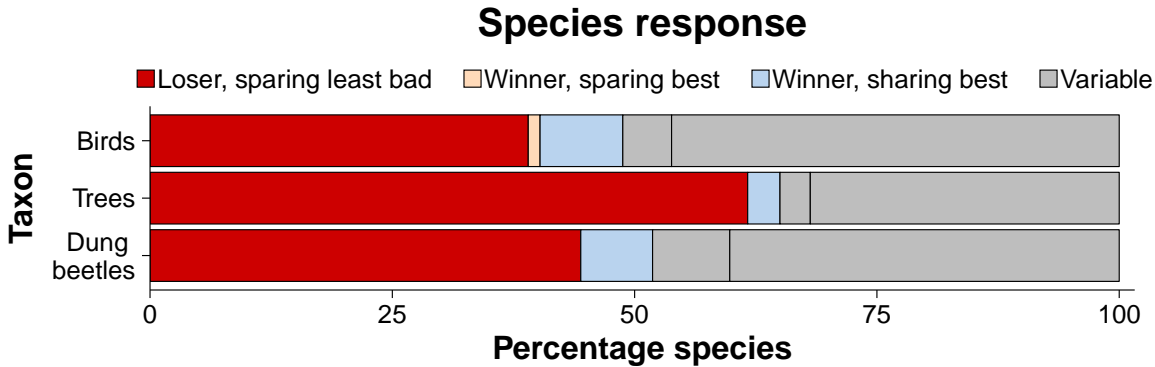
### ADDITIONAL FIGURES AND TABLES

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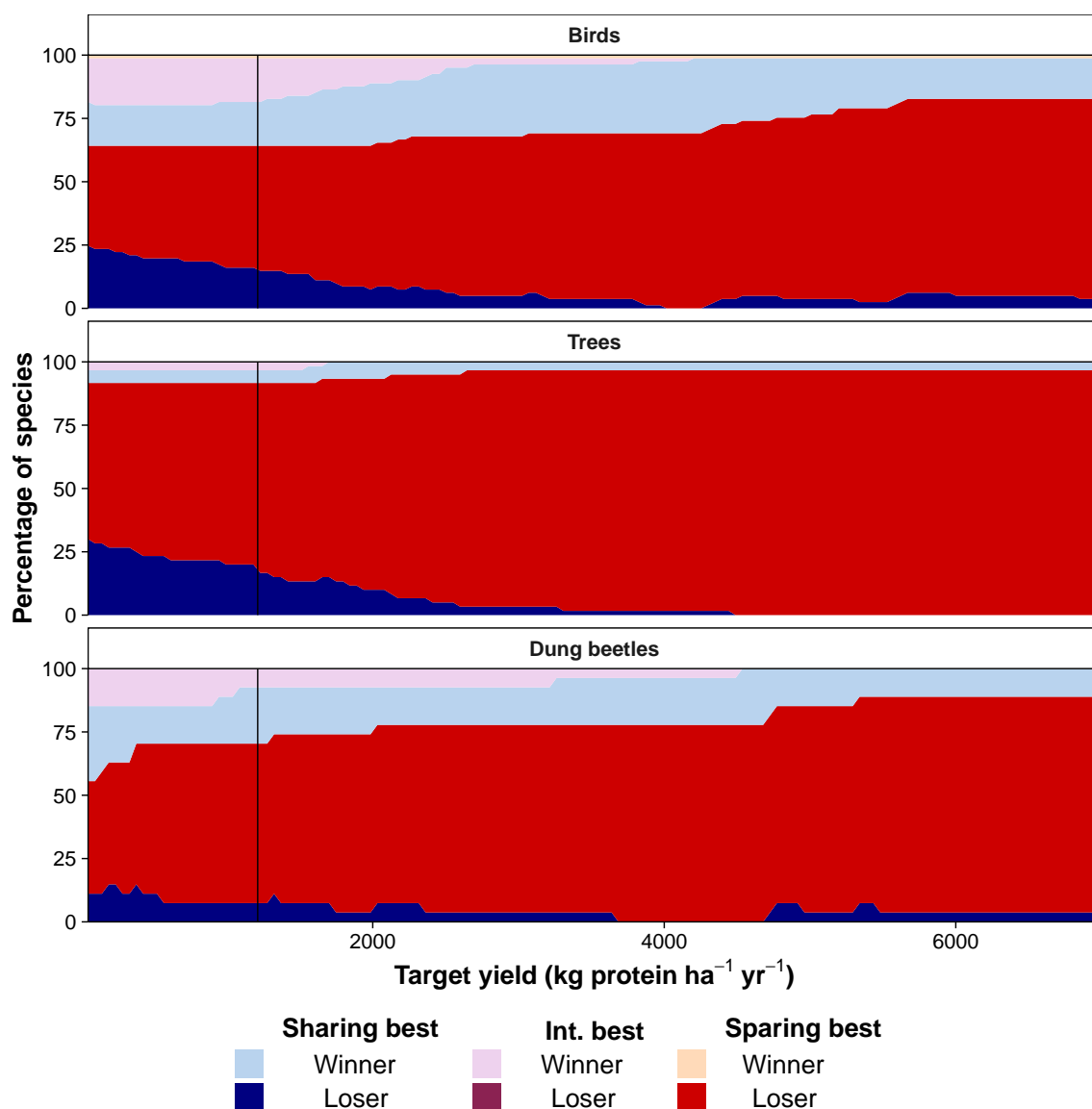
## A.1 Chapter 4: Species' responses to yields



**Fig. A.1** Example density-yield functions for six bird species showing a range of response types. Yellow-olive flycatcher and rose-throated becard are losers, with the former always doing least badly with land sparing. The latter initially does least badly with land sharing, before switching to sparing at higher yields. Botteri's sparrow and grey-crowned yellowthroat are winners favoured by land sparing and sharing respectively. Tropical mockingbird and mangrove vireo have highest densities at intermediate yields and are therefore favoured by different strategies depending on the target yield.



**Fig. A.2** The proportion of common species (those with 10 or more records) in each taxon in different response categories. Species that show “variable” responses fall into different categories depending on the production target. The black lines represent the number of species that were always winners, but which are favoured by different strategies at different production targets.



**Fig. A.3** Response categories of common species (those with 10 or more records) under different target yields. Light colours represent species that are winners, dark colours are losers. The vertical black lines represents current production: the production in Tizimín District of both calves and finished cows, divided by the land available for livestock production.

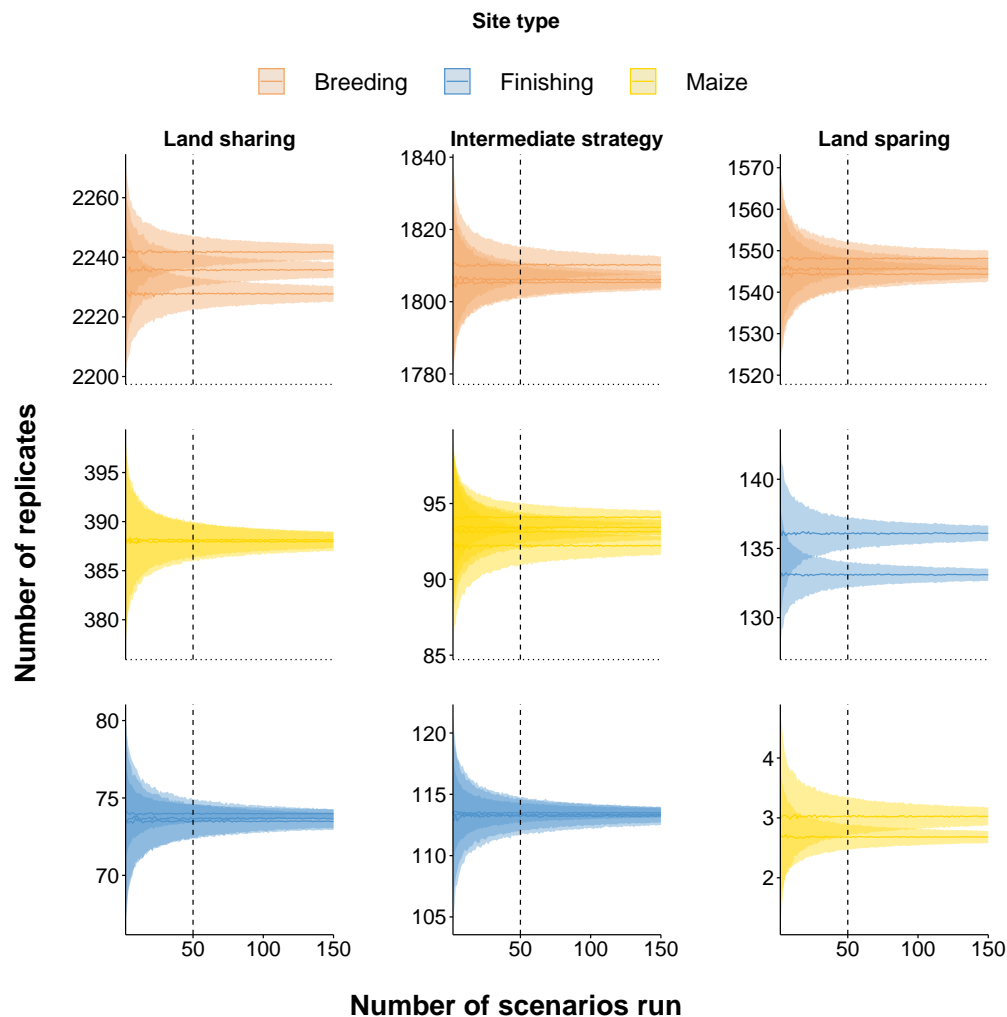


**Table A.1** The number of species detected in five or fewer sites, for which the fit of density-yield functions may be less reliable. I did not fit density-yield functions to species that were only found in baselines.

No. sites with records	Number of species		
	Birds	Trees	Dung beetles*
1	4	23	0
2	2	19	2
3	10	10	0
4	6	6	0
5	5	6	0
Spp. only in baselines	11	53	4
<b>Total no. species</b>	<b>113</b>	<b>159</b>	<b>32</b>

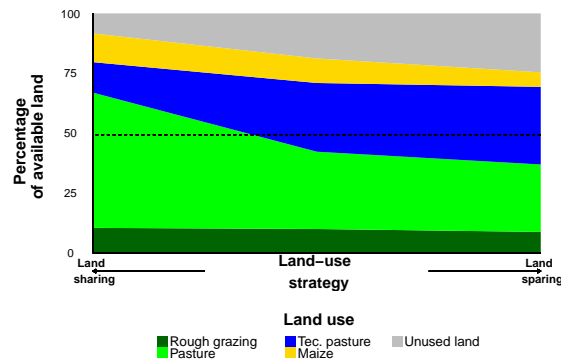
## A.2 Chapter 5: Future scenarios

### A.2.1 Bootstrapping procedure to identify the number of scenario repeats to use

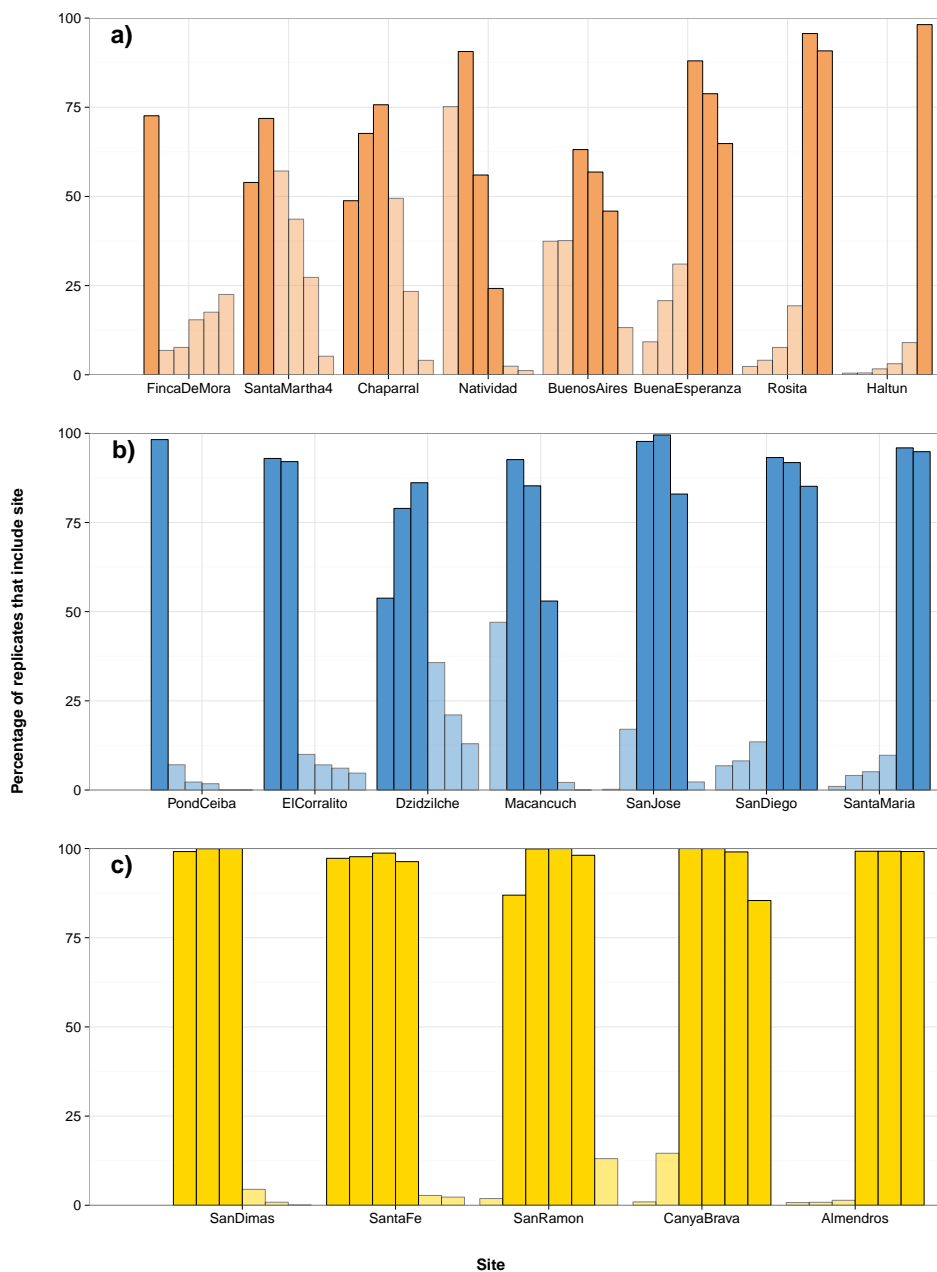


**Fig. A.4** Variation in the number of times each site was selected as I increased the number of times I ran the scenario-building process. Graphs show different land-use strategies for a production target of 100% of current production. Each line shows the mean number of times each site was picked across 1,000 random samples, with sites grouped into breeding, finishing and maize sites. The shaded area shows the standard deviation of these samples. Note the broken y-axis scales used to make variation clearer. The dashed vertical line marks 50 runs: the number I used in my final analyses.

### A.2.2 Effects of yield variations on scenarios

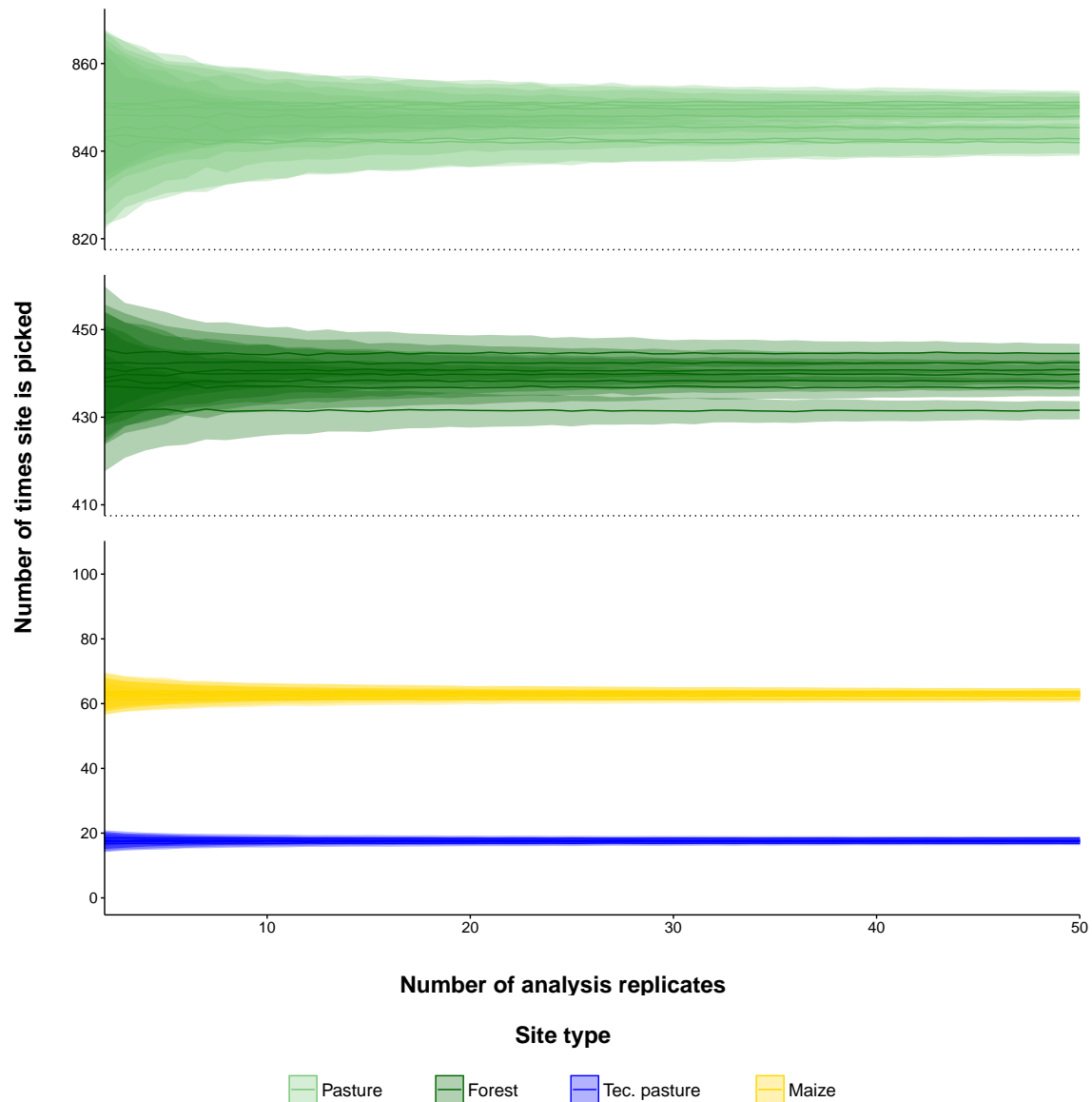


**Fig. A.5** Area of different land uses under different land-use strategies for a production target of 130% of current production but with maize yields of  $3.02 \text{ t ha}^{-1}$  (vs.  $8 \text{ t ha}^{-1}$  in the main analyses). Values are percentages of the total area of Tizimín District and the black dashed line shows the area currently under pasture, technified pasture or maize. In reality, the area under production is larger than this because some of the forest and secondary regrowth in the region will be grazed.



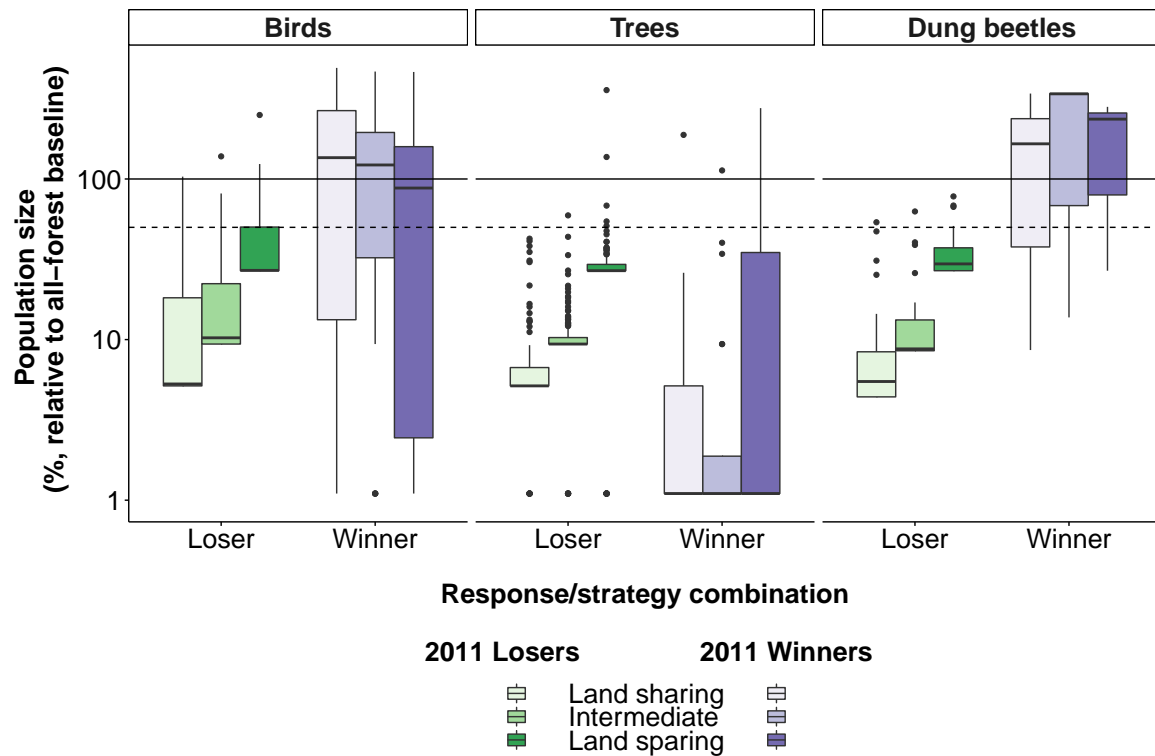
**Fig. A.6** Variation in the grouping of sites for a) breeding, b) finishing, and c) maize sites across 10,000 bootstrap runs of the Protein Production Model (Section 3.2.2). Each bar shows the percentage of runs that allocated a site to a particular land-use strategy (with strategies ordered from lowest to highest-yielding). Dark bars are those groupings used to build my scenarios, whereas light bars show variation from these.

### A.2.3 Estimating 2011 population sizes



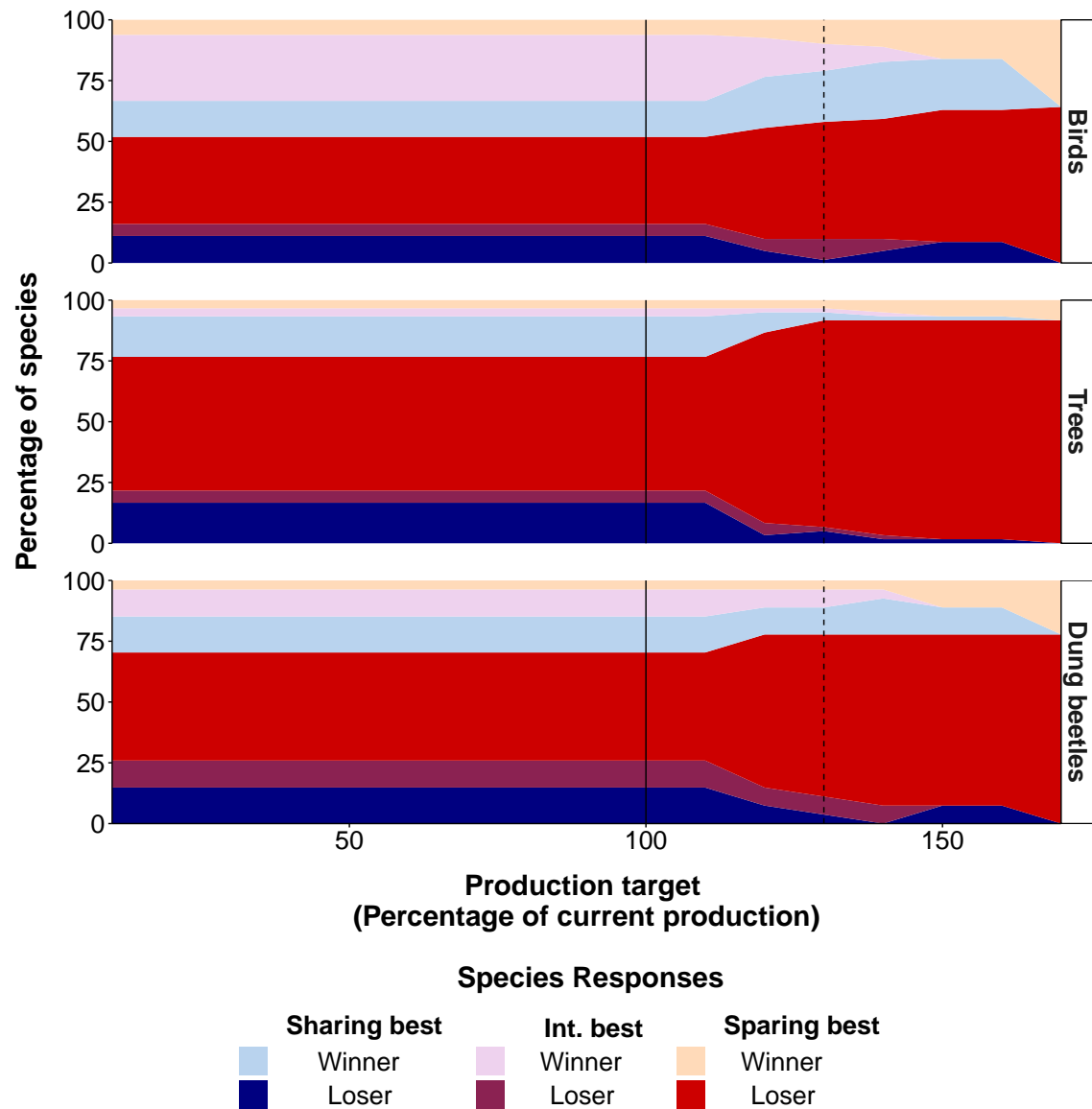
**Fig. A.7** Variation in the number of times individual study sites were picked when estimating 2011 population sizes, as the number of times I ran the analysis. Each line shows the mean number of times each site was picked across 1,000 random runs of the analysis. The shaded area shows the standard deviation of these runs. Sites are coloured based on the land use that covered the largest area within them. I have broken the y-axis for clarity: sites with large areas of pasture or forest/rough grazing were picked far more frequently because these land uses covered a far larger area of Tizimín District. See Section 5.5.1 for details on methods for estimating 2011 populations.

### A.2.4 Changing the baseline population

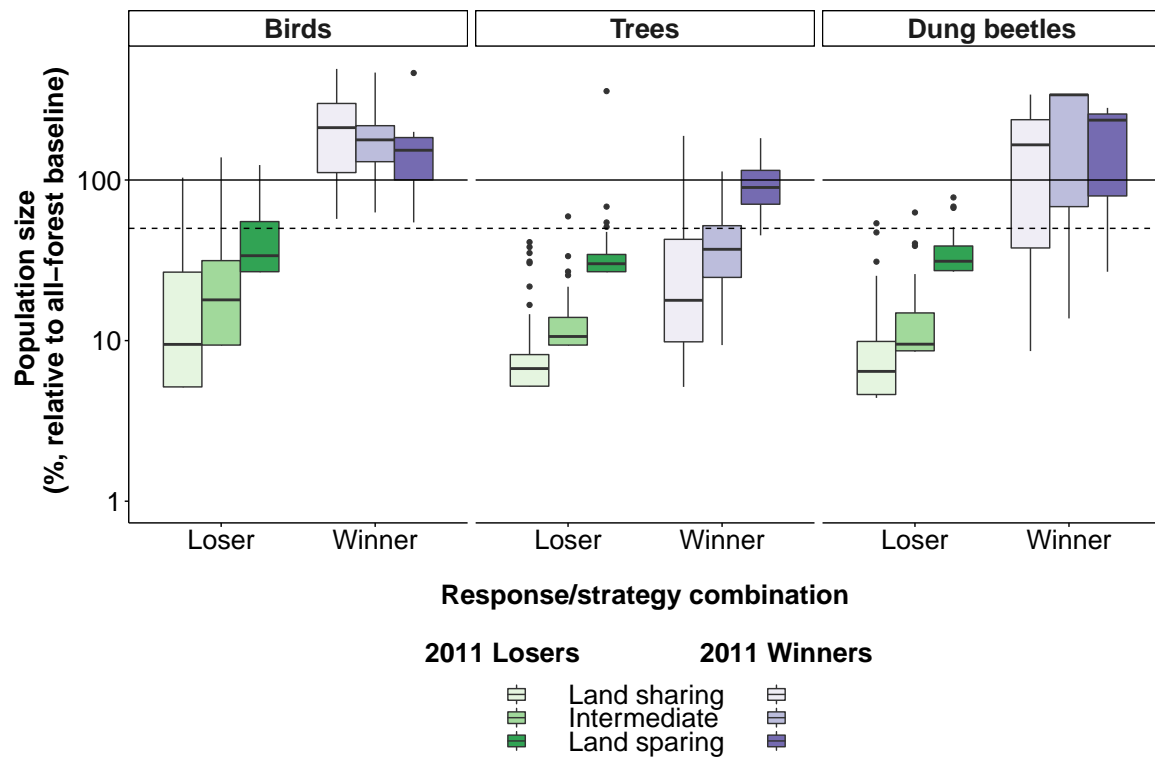


**Fig. A.8** Estimated 2030 populations of birds, trees, and dung beetles relative to an all-forest baseline under different land-use strategies, assuming a 2030 production target of 130%. Horizontal lines show the median difference in percentage size, boxes the 1<sup>st</sup> and 3<sup>rd</sup> quartiles, and vertical lines 1.5 times the interquartile range. For clarity I have used a logarithmic y-axis, truncated at 500% of baseline population sizes, although several species had larger relative populations. In addition, I have assigned an arbitrarily small population size for species absent from an all-forest baseline (23 bird species, 35 trees and two dung beetles).

### A.2.5 Excluding rare species from analyses

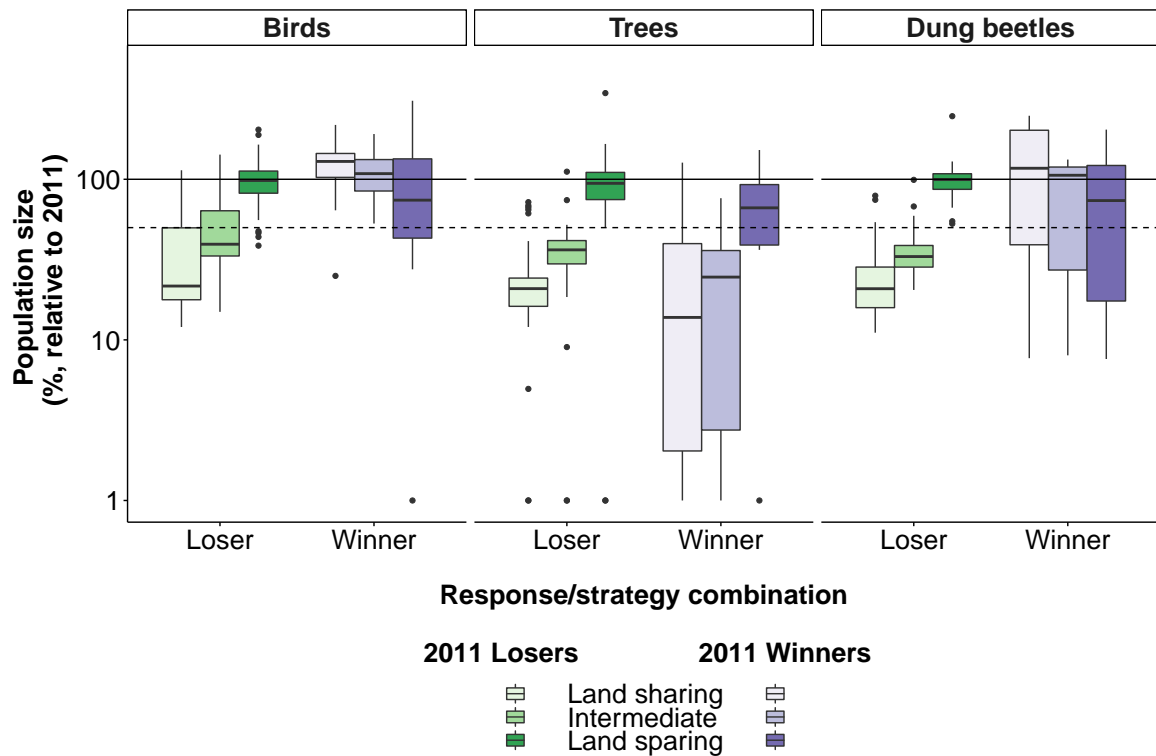


**Fig. A.9** The proportion of common species (those with 10 or more records) that show do least badly with different land-use strategies at different production targets. The solid vertical line represent current production levels, the dashed line the probable 2030 production target of 130% current production.



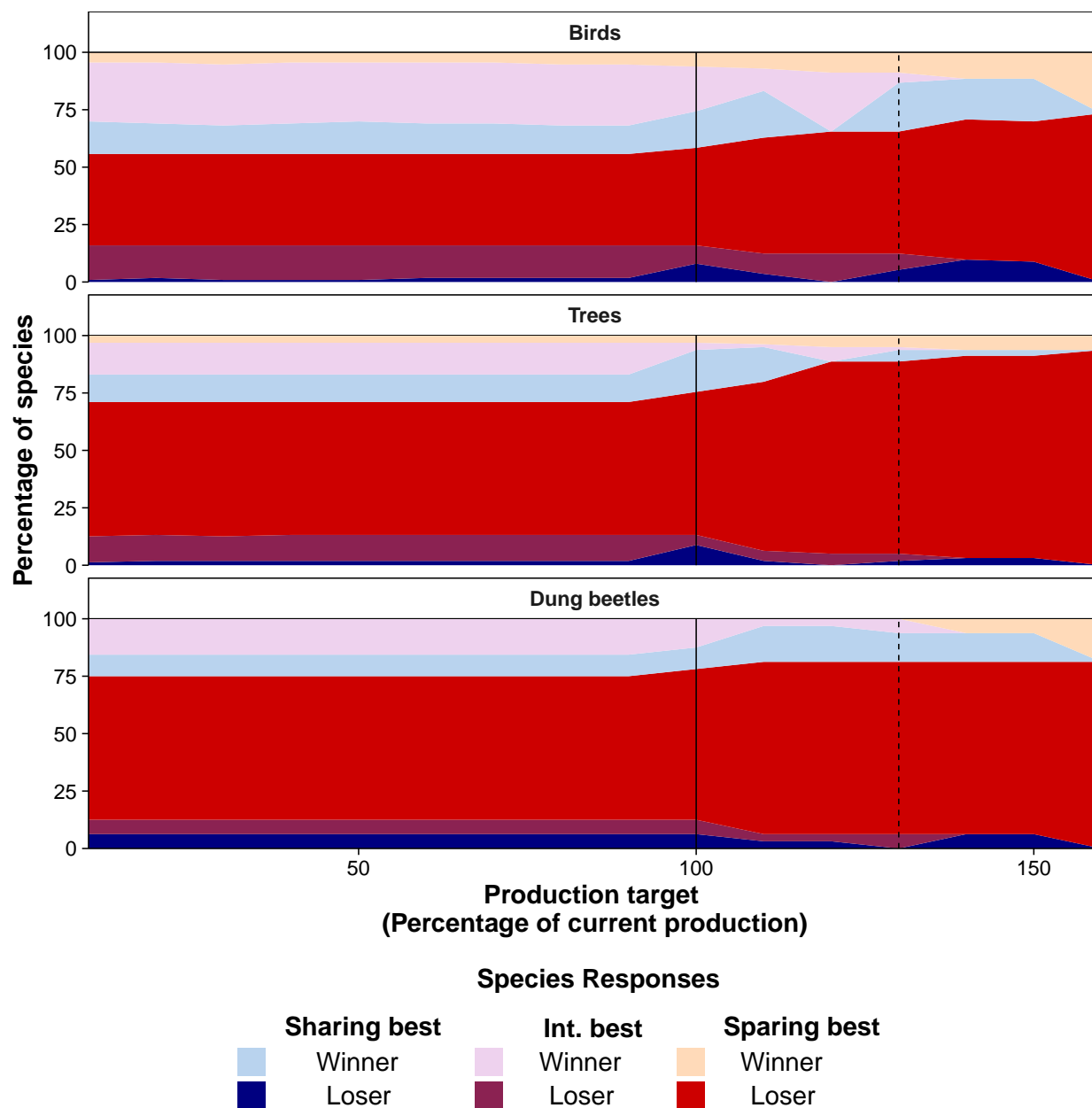
**Fig. A.10** Estimated 2030 populations of common species (those with 10 or more records) of birds, trees, and dung beetles relative to an all-forest baseline under different land-use strategies, assuming a 2030 production target of 130%. Horizontal lines show the median difference in percentage size; boxes the 1<sup>st</sup> and 3<sup>rd</sup> quartiles; and vertical lines 1.5 times the interquartile range. For clarity I have used a logarithmic y-axis, truncated at 500% of baseline population sizes, although several species had larger relative populations. In addition, I have excluded 39 species with an estimated baseline population of zero.



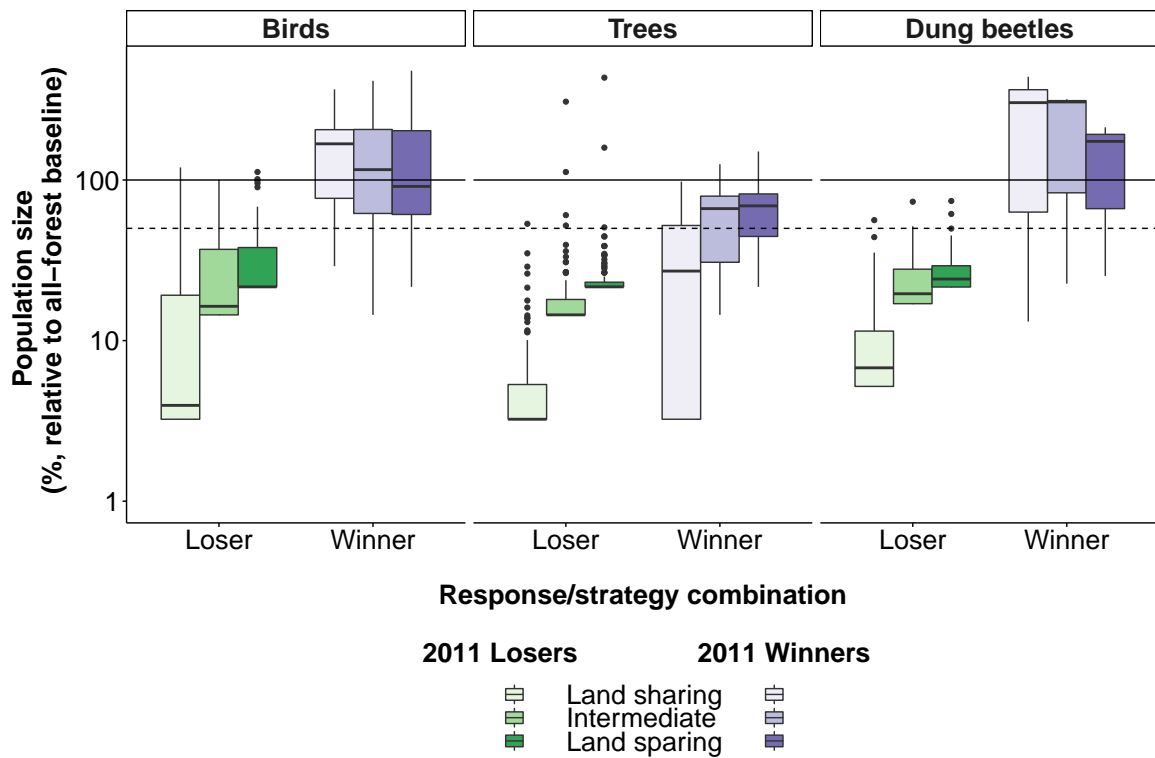


**Fig. A.11** Estimated 2030 populations of common species (those with 10 or more records) of birds, trees, and dung beetles relative to 2011 population sizes under different land-use strategies, assuming a 2030 production target of 130%. Horizontal lines show the median difference in percentage size; boxes the 1<sup>st</sup> and 3<sup>rd</sup> quartiles; and vertical lines 1.5 times the interquartile range. For clarity I have used a logarithmic y-axis, truncated at 500% of baseline population sizes, although several species had larger relative populations.

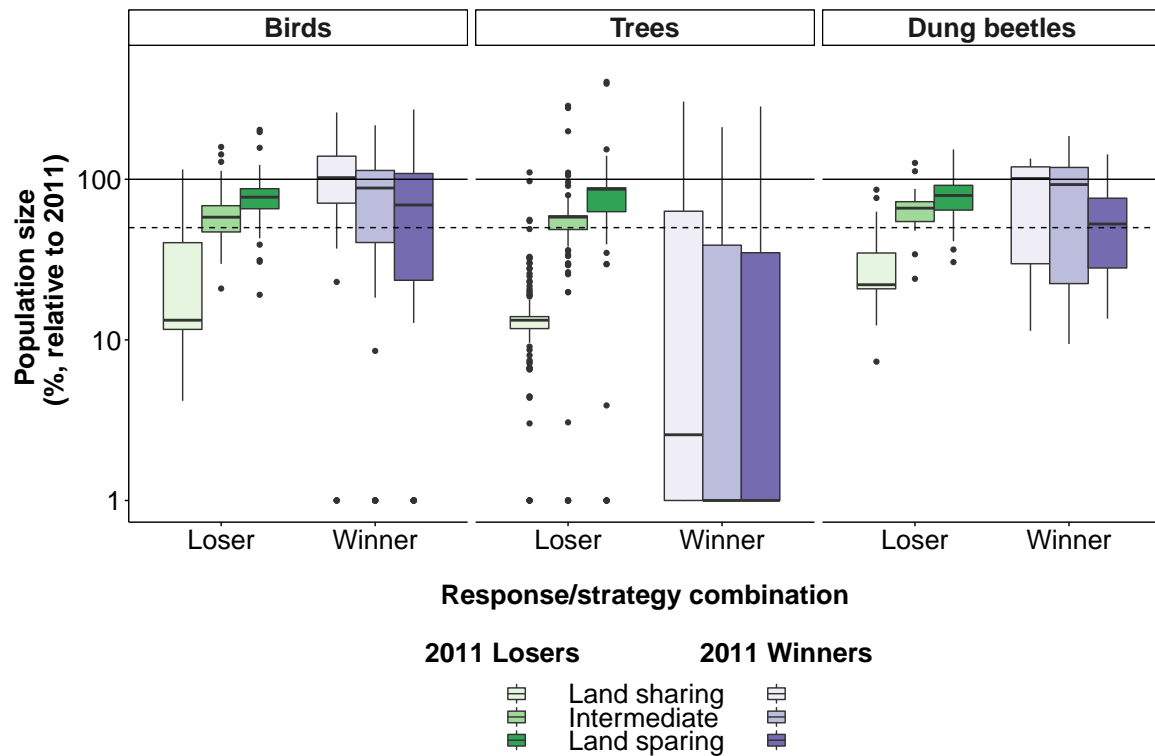
### A.2.6 Biodiversity effects of lower maize yields



**Fig. A.12** The proportion of species that show do least badly with different land-use strategies at different production targets with maize yields of  $3.02 \text{ t ha}^{-1}$  (vs.  $8 \text{ t ha}^{-1}$  in the main analyses). The solid vertical line represent current production levels, the dashed line the probable 2030 production target of 130% current production.

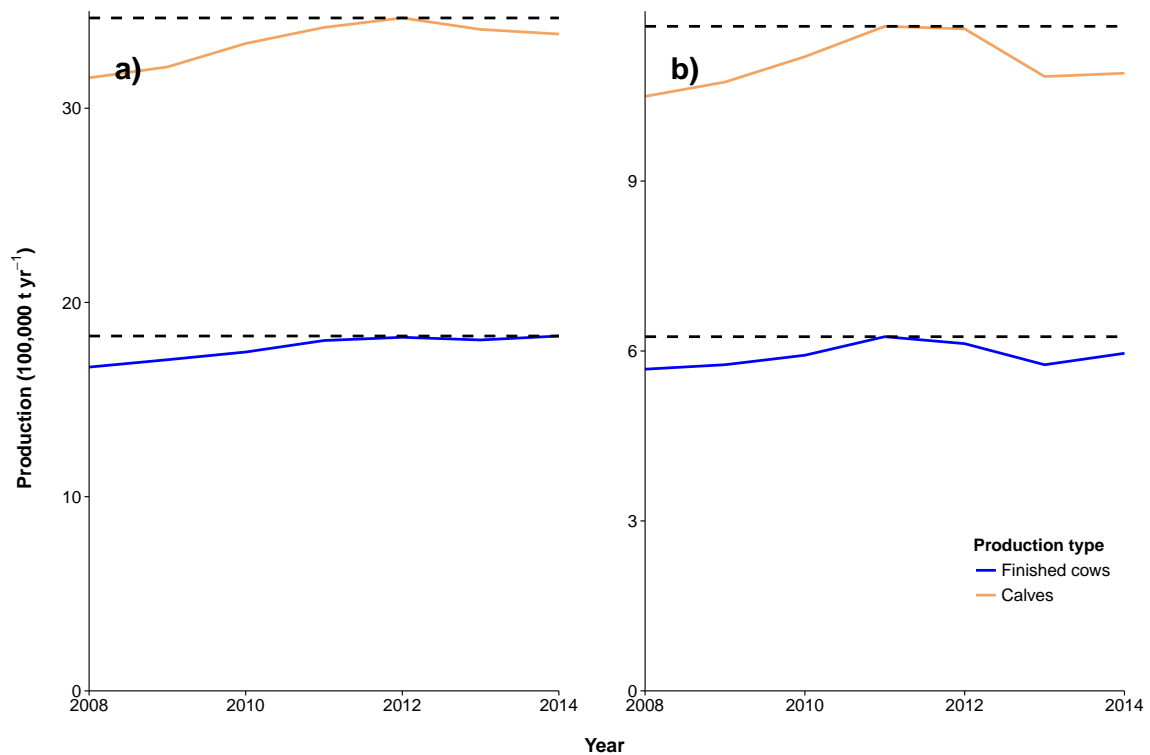


**Fig. A.13** Estimated 2030 populations of birds, trees, and dung beetles relative to an all-forest baseline under different land-use strategies, assuming a 2030 production target of 130% but with maize yields of  $3.02 \text{ t ha}^{-1}$  (vs.  $8 \text{ t ha}^{-1}$  in the main analyses). Horizontal lines show the median difference in percentage size; boxes the 1<sup>st</sup> and 3<sup>rd</sup> quartiles; and vertical lines 1.5 times the interquartile range. For clarity I have excluded 60 species with estimated baseline populations of zero and used a logarithmic y-axis, truncated at 500% of baseline population sizes, although several species had larger relative populations, and used a logarithmic y-axis.



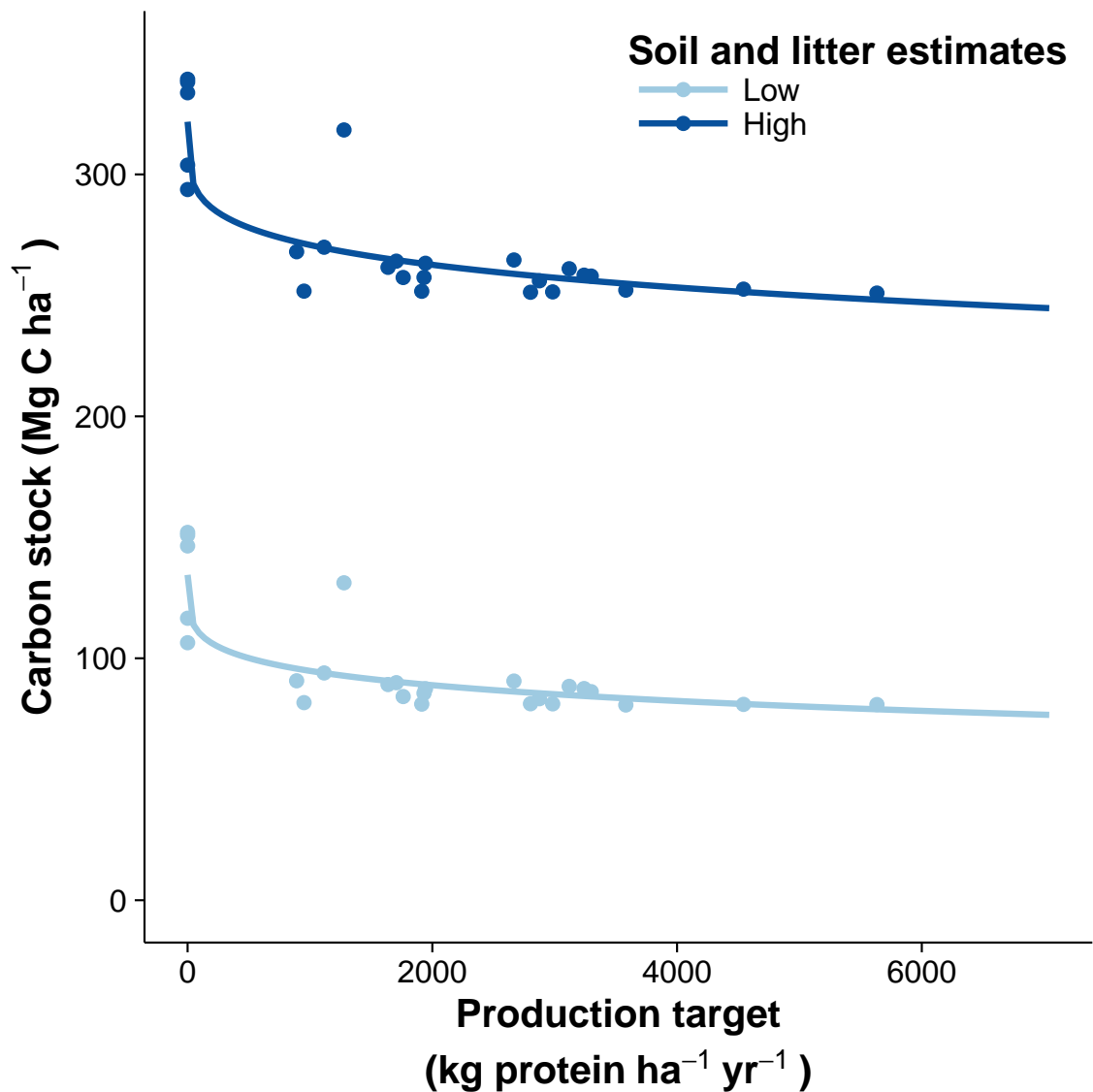
**Fig. A.14** Estimated 2030 populations of birds, trees, and dung beetles relative to 2011 under different land-use strategies, assuming a 2030 production target of 130% but with maize yields of  $3.02 \text{ t ha}^{-1}$  (vs.  $8 \text{ t ha}^{-1}$  in the main analyses). Horizontal lines show the median difference in percentage size; boxes the 1<sup>st</sup> and 3<sup>rd</sup> quartiles; and vertical lines 1.5 times the interquartile range. For clarity I have used a logarithmic y-axis, truncated at 500% of baseline population sizes, although several species had larger relative populations.

### A.2.7 Mexican cattle production

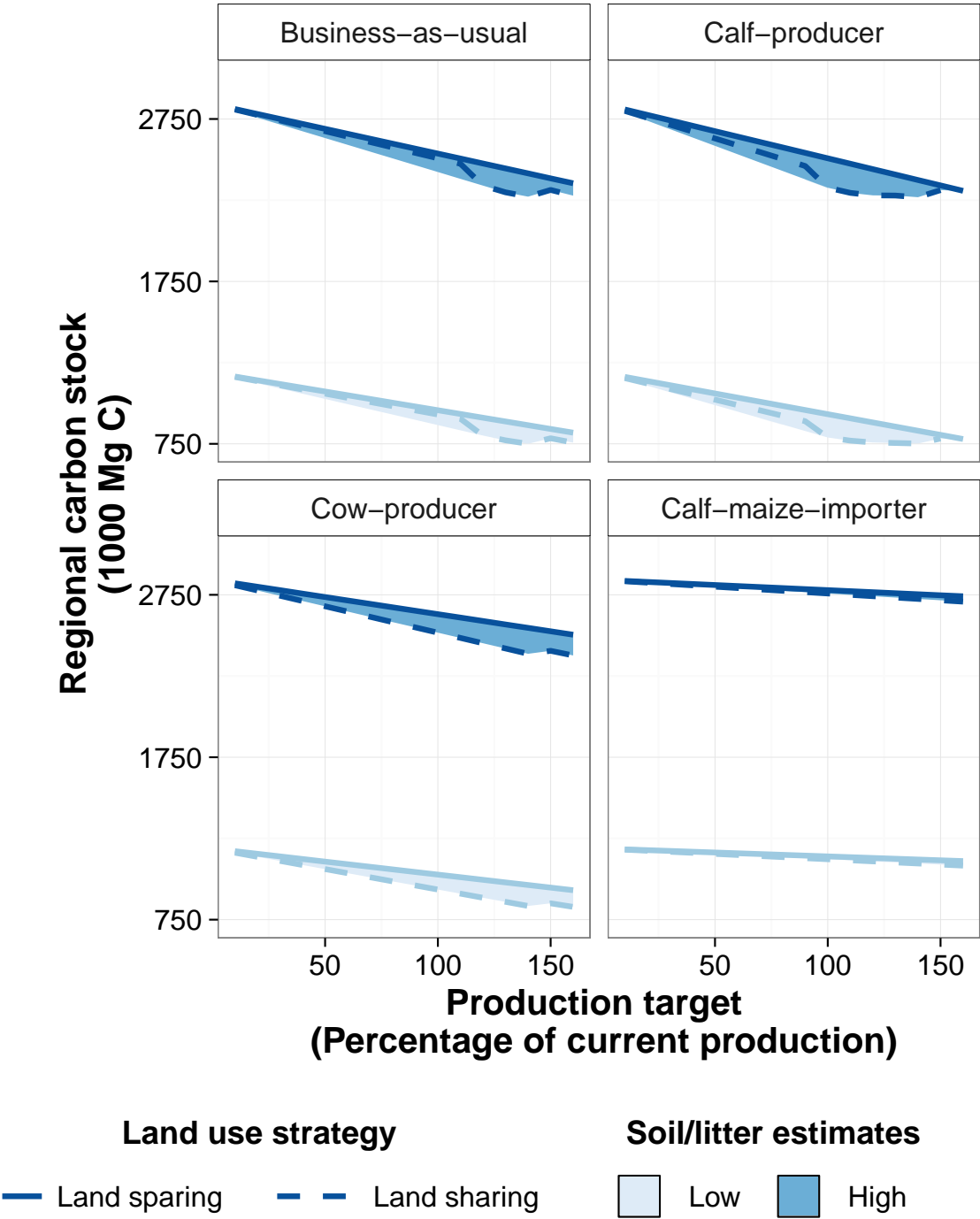


**Fig. A.15** Production of live and slaughtered animals in 2008-2014 in **a)** the whole of Mexico **b)** 11 northern states particularly badly affected by the 2012 drought. The states shown are: Aguascalientes, Baja California, Baja California Sur, Coahuila, Chihuahua, Durango, Nayarit, Nuevo León, Sinaloa, Sonora, Zacatecas. Black dashed lines show the maximum production levels for 2008–2014. Data are from (SAGARPA, 2015).

### A.3 Chapter 6: Carbon stocks and agriculture



**Fig. A.16** Density-yield function for total carbon stocks in cattle ranches in Tizimín District. Curves show combined stocks (above- and belowground biomass, standing litter crop and soil), with both high and low estimates of litter and soil stocks plotted.



**Fig. A.17** Estimated total regional carbon stocks for Tizimín District under different production systems and land-use strategies. Shaded areas show stocks under intermediate production strategies. I do not show the highest probable 2030 production target of 170% of current production because it can only be met by a land sparing strategy. In addition, for Calf-producer, only land sparing can meet a production target of 160% of current production





## APPENDIX B

### PRODUCTION AND LAND COVER DATA

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**Table B.1** Production data for breeding ranches from quantitative interviews used to fit Maize Use and Protein Production Models. Production is in kilograms of calf protein per year.

Site ID	Ranch type	Area of different land uses (ha)					Fodder inputs (t maize equivalents)	Production (kg yr <sup>-1</sup> )
		Pasture	Mec. pasture	Irigated pasture	Grazed forest	Secondary regrowth		
1	Breeding	245.0	0	105.0	50.0	0.0	330.9	2291.6
2	Breeding	52.0	0	23.0	0.0	9.0	19.0	754.0
3	Breeding	760.0	0	40.0	0.0	0.0	0.4	4683.6
4	Breeding	1010.0	0	0.0	0.0	0.0	0.5	5913.0
5	Breeding	0.0	0	19.5	0.0	0.0	336.7	2424.7
6	Breeding	1.0	0	39.0	40.0	9.0	0.0	1765.0
7	Breeding	6.5	0	0.0	0.0	0.0	9.9	187.1
8	Breeding	800.0	0	0.0	200.0	0.0	159.5	5563.6
9	Breeding	0.0	1100	0.0	80.0	0.0	326.0	12378.5
10	Breeding	190.0	0	0.0	0.0	0.0	27.8	2205.4
11	Breeding	50.0	0	0.0	53.0	0.0	9.9	569.9
12	Breeding	0.0	1050	50.0	226.0	0.0	135.3	16242.9
13	Breeding	14.0	0	0.0	2.0	0.0	12.6	478.5
14	Breeding	10.0	0	16.0	0.0	0.0	42.4	348.0
15	Breeding	40.0	0	0.0	0.0	0.0	4.4	739.5
16	Breeding	51.0	0	0.0	0.0	0.0	1.6	208.8
17	Breeding	40.0	0	10.0	0.0	60.0	32.9	957.0
18	Breeding	64.0	0	0.0	0.0	0.0	4.4	443.7
19	Breeding	28.0	0	0.0	0.0	0.0	20.7	1044.0
20	Breeding	12.0	0	0.0	0.0	0.0	6.1	87.0
21	Breeding	0.0	20	0.0	0.0	0.0	0.0	87.0
22	Breeding	200.0	0	20.0	0.0	0.0	935.2	1218.0
23	Breeding	27.0	0	0.0	0.0	0.0	144.5	261.0
24	Breeding	12.0	0	12.0	12.0	0.0	0.4	198.4
25	Breeding	300.0	0	10.0	93.5	93.5	5.2	1818.3
26	Breeding	57.0	0	2.0	40.0	180.0	4.9	495.9
27	Breeding	14.0	0	12.0	1.0	0.0	0.9	181.8
28	Breeding	10.0	0	0.0	25.0	0.0	3.1	289.3
29	Breeding	40.0	0	0.0	0.0	0.0	2.7	156.6
30	Breeding	0.0	0	24.0	0.0	0.0	73.7	113.5
31	Breeding	0.0	0	2.0	0.0	0.0	124.1	587.2
32	Breeding	37.0	0	37.0	0.0	0.0	19.3	3915.0
33	Breeding	27.0	0	10.0	0.0	0.0	0.0	380.6
34	Breeding	0.0	0	20.0	0.0	0.0	3.3	319.7
35	Breeding	0.0	0	15.0	0.0	0.0	0.0	130.5
36	Breeding	1000.0	0	0.0	0.0	0.0	23.7	11255.6
37	Breeding	450.0	0	89.5	187.0	0.0	108.3	9008.9
38	Breeding	25.0	0	25.0	0.0	0.0	158.9	1737.7
39	Breeding	146.0	80	0.0	0.0	30.0	127.8	1934.6
40	Breeding	55.0	0	15.0	30.0	0.0	52.0	348.0
41	Breeding	354.0	0	0.0	0.0	0.0	26.4	2122.8
42	Breeding	200.0	0	0.0	0.0	0.0	8.0	1461.6
43	Breeding	60.0	0	17.8	50.0	0.0	197.2	2427.3
44	Breeding	176.0	0	21.0	0.0	0.0	24.9	2392.5
45	Breeding	257.0	0	120.0	3.0	0.0	22.4	2631.8
46	Breeding	36.0	0	0.0	11.0	0.0	11.0	320.2
47	Breeding	160.0	0	0.0	0.0	0.0	16.7	2320.7
48	Breeding	280.0	0	0.0	0.0	0.0	0.0	2509.9
49	Breeding	240.0	0	30.0	0.0	0.0	72.6	3772.1

**Table B.2** Production data for finishing ranches from quantitative interviews used to fit Maize Use and Protein Production Models. Production is in kilograms of finished cow protein per year.

Site ID	Ranch type	Area of different land uses (ha)					Fodder inputs (t maize equivalents)	Production (kg yr <sup>-1</sup> )
		Pasture	Mec. pasture	Irigated pasture	Grazed forest	Secondary regrowth		
50	Finishing	674.0	0	26.0	0.0	0.0	7478.8	52495.8
51	Finishing	16.8	0	0.0	3.2	0.0	4.6	630.8
52	Finishing	3.7	0	0.0	0.0	0.0	1392.3	7755.6
53	Finishing	152.0	0	0.0	0.0	0.0	0.0	3364.0
54	Finishing	18.0	0	3.0	0.0	0.0	230.4	11198.6
55	Finishing	124.0	0	0.0	0.0	30.0	186.4	2349.0
56	Finishing	44.5	0	0.0	15.0	0.0	123.6	762.1
57	Finishing	5.0	0	0.0	0.0	0.0	80.8	319.7
58	Finishing	0.0	0	135.0	0.0	0.0	237.3	9165.5
59	Finishing	0.0	0	30.0	0.0	0.0	234.6	7612.5
60	Finishing	0.0	0	34.0	0.0	0.0	104.4	5731.1
61	Finishing	0.0	190	0.0	0.0	0.0	71.1	10388.0
62	Finishing	15.0	0	0.0	0.0	45.0	9.6	346.0
63	Finishing	42.0	0	0.0	0.0	0.0	0.0	715.6
64	Finishing	19.5	0	0.0	2.0	0.0	31.2	1252.8
65	Finishing	4.0	0	14.0	8.0	0.0	18.3	548.1
66	Finishing	0.0	0	16.0	0.0	0.0	17.1	743.9
67	Finishing	18.0	0	30.0	0.0	0.0	7.7	1686.1
68	Finishing	0.0	0	15.0	0.0	0.0	50.0	730.8
69	Finishing	16.0	0	0.0	0.0	0.0	3.5	561.1
70	Finishing	68.0	0	0.0	0.0	0.0	29.2	3588.8
71	Finishing	0.0	0	22.0	0.0	10.0	53.7	1402.9
72	Finishing	8.0	0	15.0	1.0	0.0	11.0	613.4
73	Finishing	0.0	0	15.0	0.0	0.0	36.3	626.4
74	Finishing	30.0	0	0.0	0.0	20.0	6.9	1305.0
75	Finishing	23.0	7	50.0	0.0	0.0	606.7	8752.2
76	Finishing	25.0	0	0.0	0.0	0.0	32.8	1061.4
77	Finishing	83.7	50	15.0	0.0	0.0	55.7	2392.5

**Table B.3** Areas of different land uses in the 20 productive study sites. SP refers to silvopastoral study sites.

Site	Area of land use (ha)												
	In breeding ranches					In finishing ranches					In maize ranches		No production
	Pasture	Mec. pasture	Irrigated pasture	Grazed forest	Secondary regrowth	Pasture	Mec. pasture	Irrigated pasture	Grazed forest	Secondary regrowth	Maize	Hay grass	
Traditional 1	80.3	0.0	0.0	15.9	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	3.8
Traditional 2	54.8	24.5	0.0	1.3	3.6	3.6	0	0.0	6.9	0.0	0.0	0.0	5.3
Traditional 3	96.4	0.0	0.0	3.2	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.4
Traditional 4	0.8	0.0	0.0	99.2	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0
Traditional 5	0.0	73.1	0.0	4.6	0.0	0.0	0	0.0	0.0	0.0	0.0	22.3	0.0
Traditional 6	10.6	0.0	0.0	23.2	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	17.8
Traditional 7	0.2	76.8	0.0	23.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0
SP 1	42.2	0.0	13.4	5.3	7.1	0.0	0	0.0	0.0	0.0	0.0	2.3	15.2
SP 2	0.0	0.0	0.0	0.0	0.0	72.2	0	0.0	0.0	25.8	0.0	0.0	2.0
SP 3	20.3	0.0	7.6	3.3	0.0	23.5	0	0.0	11.2	0.0	2.9	0.0	31.2
SP 4	47.0	0.0	5.0	24.1	9.0	0.0	0	0.0	0.0	8.9	1.0	4.0	0.9
<i>Tecnificado 1</i>	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	17.0
<i>Tecnificado 2</i>	0.0	0.0	0.0	0.0	0.0	0.3	0	79.7	0.0	0.0	0.0	0.0	19.9
<i>Tecnificado 3</i>	16.7	21.6	0.0	2.5	2.2	1.7	0	28.0	0.7	0.0	9.0	1.0	16.6
<i>Tecnificado 4</i>	0.0	0.0	0.0	0.0	0.0	0.0	99	0.0	0.0	0.0	0.0	0.0	1.0
Maize 1	0.0	0.0	0.0	0.0	0.0	25.7	0	1.4	0.0	5.2	33.1	21.0	13.6
Maize 2	0.0	0.0	0.0	0.0	0.0	10.6	0	0.0	1.4	0.0	51.5	19.4	17.2
Maize 3	0.0	0.0	0.0	0.0	0.0	12.7	0	0.0	9.9	0.0	29.9	9.8	37.7
Maize 4	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	72.3	3.1	10.7
Maize 5	21.6	0.0	15.2	1.1	0.0	4.6	0	0.0	0.0	0.0	28.9	16.8	11.7

## APPENDIX C

### COUNTS OF BIRDS, TREES AND DUNG BEETLES IN STUDY SITES

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**Table C.1** Counts (C), effective detection radii (EDA) and densities (D) of bird species in baseline and traditional ranch sites.

Species	Baseline sites												Traditional ranches																								
	1			2			3			4			5			1			2			3			4			5			6			7			
	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D				
Altamira oriole	12	0.3	43.2	3	0.3	2.8	4	0.3	14.4	8	0.3	7.4	2	0.3	7.2	4	0.3	3.5	4	0.3	14.3	18	0.3	16.8	1	0.3	3.4	2	0.3	1.9	2	0.3	6.9	5	0.3	4.6	
Barred antshrike	2	0.4	5.7	0	0.4	0.0	1	0.4	2.8	0	0.4	0.0	0	0.4	0.0	2	0.4	1.9	0	0.4	0.0	4	0.4	3.8	1	0.4	2.8	1	0.4	1.0	0	0.4	0.0	1	0.4	1.0	
Black catbird	0	0.0	0.0	2	0.0	1.9	2	0.0	106.1	5	0.0	4.8	8	0.0	424.3	0	0.0	0.0	0	0.0	0.0	2	0.0	1.8	2	0.0	232.7	0	0.0	0.0	2	0.0	171.4	2	0.0	2.0	
Black-bellied whistling-duck	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	
Black-cowbird oriole	1	0.1	16.0	0	0.1	0.0	0	0.1	0.0	3	0.1	3.0	0	0.1	0.0	0	0.0	0.0	0	0.0	0.0	1	0.1	0.9	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	
Black-faced antthrush	0	0.4	0.0	1	0.4	1.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	
Black-headed saltator	4	0.4	19.7	2	0.4	1.1	2	0.4	9.9	2	0.4	1.1	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	1	0.4	4.9	1	0.4	0.5	2	0.4	9.9	2	0.4	1.1	
Black-headed tanager	0	0.4	0.0	10	0.4	8.2	0	0.4	0.0	1	0.4	0.8	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	1	0.4	0.8	0	0.4	0.0	0	0.4	0.0	
Black-throated bobwhite	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	4	0.4	2.6	21	0.4	88.9	0	0.4	0.0	5	0.4	21.2	16	0.4	10.2	8	0.4	33.9	1	0.4	0.6	
Blue bunting	2	0.2	12.3	18	0.2	17.6	10	0.2	61.7	5	0.2	4.9	3	0.2	18.5	1	0.2	1.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	
Blue-black grassquit	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	18	0.1	7.3	53	0.1	1373.2	0	0.0	0.0	11	0.1	151.7	4	0.1	37.4	17	0.1	294.4	18	0.1	12.3	
Blue-crowned motmot	6	0.4	18.6	6	0.4	5.2	6	0.4	18.6	11	0.4	9.6	8	0.4	24.8	0	0.4	0.0	0	0.4	0.0	5	0.4	4.4	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	
Blue-grey gnatcatcher	0	0.0	0.0	1	0.0	0.9	2	0.0	106.8	5	0.0	4.3	1	0.0	32.4	4	0.1	0.7	6	0.1	290.3	2	0.0	1.9	3	0.1	28.4	19	0.1	20.9	13	0.1	195.4	5	0.1	3.5	
Blue-grey tanager	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	
Boat-billed flycatcher	1	0.3	4.5	1	0.3	0.7	0	0.3	0.0	3	0.3	2.2	4	0.3	18.1	0	0.4	0.0	0	0.4	0.0	1	0.3	0.7	0	0.4	0.0	1	0.4	0.8	0	0.3	0.0	0	0.4	0.0	
Botter's sparrow	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	6	0.2	8.2	6	0.2	27.9	0	0.2	0.0	3	0.2	20.9	2	0.2	1.6	3	0.2	17.5	8	0.2	7.7	
Bright-rumped attila	2	0.4	5.8	0.4	8.5	6	0.4	17.4	4	0.4	3.8	0.4	11.6	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	2	0.4	1.9	0	0.4	0.0	1	0.4	0.8	0	0.4	2.9	0	0.4	0.0
Bronzed cowbird	0	0.1	0.0	0	0.1	0.0	0	0.1	0.0	2	0.1	0.3	0	0.1	0.0	3	0.1	0.1	2	0.3	129.6	0	0.1	0.0	0	0.1	0.0	2	0.3	38.8	1	0.3	0.2	0	0.2	0.0	
Brown jay	0	0.1	0.0	4	0.1	2.7	2	0.1	32.6	1	0.1	0.7	0	0.1	0.0	0	0.0	0.0	0	0.0	0.0	0	0.1	0.0	0	0.0	0.0	0	0.0	0.0	0	0.1	0.0	0	0.1	0.0	
Brown-crested flycatcher	0	0.1	0.0	0	0.1	0.0	1	0.1	13.8	0	0.1	0.0	2	0.1	27.6	2	0.2	0.8	1	0.2	13.0	5	0.1	4.5	1	0.2	6.0	5	0.2	4.9	0	0.1	0.0	6	0.2	4.6	
Buff-bellied hummingbird	1	0.0	47.7	1	0.0	1.0	0	0.0	0.0	1	0.0	1.0	3	0.0	143.1	0	0.1	0.0	0	0.1	0.0	1	0.0	1.1	0	0.1	0.0	0	0.1	0.0	0	0.1	0.0	0	0.1	0.0	
Canivet's Emerald	1	0.0	210.6	0	0.0	0.0	2	0.0	421.2	1	0.0	0.0	2	0.0	42.2	0	0.0	0.0	0	0.0	0.0	5	0.0	5.3	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	
Caribbean dove	0	0.4	0.0	12	0.4	11.4	0	0.4	0.0	1	0.4	1.0	4	0.4	11.4	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	
Carolina wren	10	0.2	44.4	21	0.2	21.0	26	0.2	115.5	20	0.2	20.0	20	0.2	88.9	0	0.2	0.0	0	0.2	0.0	10	0.2	9.9	0	0.2	0.0	0	0.2	0.0	3	0.2	14.7	4	0.2	4.1	
Cinnamon hummingbird	1	0.0	124.0	1	0.0	1.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	1	0.0	0.3	2	0.0	227.1	0	0.0	0.0	0	0.0	0.0	1	0.0	1.2	0	0.0	0.0	0	0.0	0.0	
Clay-colored robin	7	0.4	20.1	30	0.4	28.3	13	0.4	37.3	19	0.4	17.9	28	0.4	80.3	3	0.2	4.2	0	0.2	0.0	28	0.4	25.1	3	0.2	13.7	1	0.3	0.8	11	0.3	10.7	11	0.3	10.7	
Common ground-dove	0	0.3	0.0	0	0.3	0.0	0	0.3	0.0	1	0.3	0.7	0	0.3	0.0	1	0.2	1.1	3	0.2	14.6	0	0.3	0.0	1	0.2	8.6	5	0.2	2.8	5	0.3	33.5	1	0.2	0.7	
Couch's kingbird	3	0.4	10.3	3	0.4	2.4	2	0.4	6.9	3	0.4	2.4	4	0.4	13.8	3	0.2	4.1	3	0.2	11.4	4	0.4	2.9	7	0.2	48.3	2	0.2	1.3	1	0.3	5.3	3	0.2	2.4	
Dusky-capped flycatcher	7	0.4	19.8	3	0.4	2.9	6	0.4	17.0	4	0.4	3.9	7	0.4	19.8	3	0.1	7.8	2	0.1	6.8	7	0.4	5.7	4	0.1	38.8	0	0.2	0.0	2	0.3	12.0	2	0.2	1.9	
Eastern meadowlark	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	
Ferruginous pygmy-owl	2	0.4	5.4	0	0.4	0.0	0	0.4	0.0	1	0.4	1.0	0	0.4	0.0	0	0.4	1.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	1	0.4	1.0	1	0.4	2.7	0	0.4	0.0	
Gartered trogon	0	0.4	0.0	3	0.4	3.0	2	0.4	5.4	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	
Golden-fronted woodpecker	4	0.4	11.8	11	0.4	10.1	6	0.4	17.7	10	0.4	9.2	4	0.4	11.8	2	0.3	2.0	3	0.3	9.0	7	0.4	6.3	3	0.3	10.0	8	0.3	7.1	4	0.4	12.7	12	0.3	11.1	
Golden-olive woodpecker	0	0.3	0.0	0	0.3	0.0	5	0.3	14.4	2	0.3	2.0	4	0.3	11.5	0	0.2	1.5	0	0.2	0.0	0	0.3	0.0	1	0.2	4.7	0	0.2	0.0	0	0.3	0.0	0	0.3	0.0	
Great kiskadee	0	0.4	0.0	0	0.4	0.0	2	0.4	6.5	0	0.4	0.0	0	0.4	0.0	0	0.4	1.7	1	0.4	3.2	1	0.4	0.8	0	0.4	0.0	2	0.4	1.7	0	0.4	0.0	0	0.4	0.0	
Great-tailed grackle	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	4	0.2	1.2	0	0.3	0.0	0	0.2	0.0	0	0.2	0.0	1	0.2	0.5	0	0.2	0.0	0	0.2	0.0	
Green jay	3	0.4	10.4	0	0.4	0.0	0	0.4	0.0	1	0.4	0.8	0	0.4	0.0	1	0.4	0.8	1	0.4	3.5	4	0.4	3.1	0	0.4	0.0	1	0.4	0.8	0	0.4	0.0	0	0.4	0.0	
Green-backed sparrow	4	0.2	20.2	3	0.2	3.0	8	0.2	40.3	10	0.2	10.0	0	0.2	0.0	0	0.3	0.0	0	0.3	0.0	6	0.2	6.2	0	0.3	0.0	0	0.3	0.0	0	0.2	0.0	0	0.3	0.0	

**Table C.2** Counts (C), effective detection radii (EDA) and densities (D) of bird species in silvopastoral, *tecnificado* and maize sites.

Species	Silvopastoral sites												Tecnificado sites												Maize sites														
	1			2			3			4			1			2			3			4			1			2			3			4			5		
	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D	C	EDA	D						
Altamira oriole	3	0.3	10.4	2	0.3	1.8	11	0.3	38.5	2	0.3	1.8	5	0.3	17.2	1	0.3	0.9	2	0.3	6.9	0	0.3	0.0	3	0.3	10.4	0	0.2	0.0	3	0.3	8.0	0	0.3	0.0	0	0.3	0.0
Barred antshrike	0	0.4	0.0	4	0.4	3.8	3	0.4	8.5	1	0.4	1.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.2	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Black catbird	1	0.0	83.8	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Black-bellied whistling-duck	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	4	0.4	147.2	0	0.3	0.0	1	0.4	27.6	0	0.4	0.0	0	0.4	0.0
Black-cowbird oriole	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Black-faced antthrush	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Black-headed saltator	0	0.4	0.0	0	0.4	0.0	5	0.4	24.7	2	0.4	1.1	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Black-headed trogon	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Black-throated bobwhite	12	0.4	50.8	22	0.4	14.1	3	0.4	12.7	3	0.4	19.8	8	0.4	33.9	3	0.4	1.9	4	0.4	16.9	5	0.4	3.2	15	0.4	63.5	12	0.3	10.2	12	0.4	38.1	3	0.4	2.6	9	0.4	28.6
Blue bunting	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.1	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0
Blue-black grassquit	19	0.1	338.3	64	0.1	42.2	20	0.1	395.9	20	0.1	13.6	5	0.1	81.6	5	0.1	3.4	32	0.1	531.7	25	0.1	15.6	27	0.1	227.4	32	0.1	25.8	53	0.1	874.9	38	0.1	31.1	21	0.1	274.6
Blue-crowned motmot	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	2	0.4	1.7	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Blue-grey gnatcatcher	10	0.1	161.3	14	0.1	8.9	8	0.1	162.7	13	0.1	8.7	4	0.1	55.4	1	0.1	0.7	4	0.1	57.3	1	0.1	0.6	3	0.1	49.4	0	0.1	0.0	9	0.1	167.5	0	0.1	0.0	3	0.1	35.2
Blue-grey tanager	1	0.4	2.7	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	5	0.4	0.0	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Boat-billed flycatcher	0	0.3	0.0	0	0.4	0.0	3	0.3	12.5	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.3	0.0	0	0.3	0.0	0	0.3	0.0	0	0.3	0.0
Botter's sparrow	5	0.2	28.8	3	0.2	2.9	1	0.2	5.3	0	0.2	0.0	1	0.2	6.3	7	0.2	6.8	5	0.2	30.8	15	0.2	15.6	10	0.2	57.3	1	0.1	1.4	4	0.2	14.5	12	0.2	16.9	9	0.2	39.8
Bright-rumped attila	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Bronzed cowbird	2	0.3	59.9	0	0.3	0.0	2	0.2	72.1	2	0.2	6.3	3	0.3	78.7	3	0.3	0.4	2	0.3	54.0	1	0.3	0.1	19	0.3	576.6	3	0.2	0.4	5	0.2	159.7	3	0.2	0.4	3	0.3	65.3
Brown jay	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	1	0.0	52.4	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Brown-crested flycatcher	3	0.2	24.5	2	0.2	1.5	2	0.1	18.5	4	0.1	3.0	5	0.2	37.0	5	0.2	3.7	2	0.2	15.1	0	0.2	0.0	1	0.2	8.2	0	0.1	0.0	3	0.1	23.6	1	0.1	0.9	9	0.2	53.7
Buff-bellied hummingbird	0	0.0	0.0	0	0.1	0.0	1	0.0	28.3	0	0.0	0.0	0	0.1	0.0	0	0.1	0.0	0	0.1	0.0	0	0.1	0.0	0	0.1	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.1	0.0
Cassini's Elaenia	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	2	0.0	166.3	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0
Caribbean dove	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Carolina wren	0	0.2	0.0	0	0.2	0.0	1	0.2	4.8	0	0.2	0.0	1	0.2	5.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.1	0.0	1	0.2	3.5	0	0.2	0.0	0	0.2	0.0
Cinnamon hummingbird	2	0.0	96.2	0	0.0	0.0	1	0.0	58.7	2	0.0	1.6	0	0.0	0.0	1	0.0	0.8	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	2	0.0	69.8
Clay-coloured robin	2	0.3	3.8	0	0.3	0.0	16	0.3	55.6	7	0.3	6.8	3	0.3	12.2	1	0.2	1.0	2	0.3	8.0	0	0.2	0.0	0	0.3	0.0	0	0.2	0.0	1	0.3	2.3	0	0.3	0.0	1	0.2	2.9
Common ground-dove	3	0.2	19.7	7	0.2	5.0	4	0.2	23.6	0	0.2	0.0	1	0.2	7.4	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	4	0.2	26.0	0	0.1	0.0	4	0.2	15.2	0	0.2	0.0	2	0.2	10.2
Couch's kingbird	8	0.2	41.1	4	0.2	3.4	2	0.3	9.0	4	0.3	3.3	10	0.2	57.2	5	0.2	4.2	2	0.2	11.1	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	1	0.3	2.8	1	0.3	1.3	5	0.2	19.0
Dusky-capped flycatcher	0	0.2	0.0	0	0.2	0.0	2	0.2	9.6	3	0.2	2.9	2	0.1	15.1	0	0.1	0.0	1	0.1	7.2	0	0.1	0.0	0	0.1	0.0	0	0.1	0.0	0	0.2	0.0	0	0.1	0.0	0	0.1	0.0
Eastern meadowlark	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Ferruginous pygmy-owl	0	0.4	0.0	0	0.4	0.0	1	0.4	2.7	1	0.4	1.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Gartered trogon	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0	0	0.3	0.0	0	0.4	0.0	0	0.4	0.0	0	0.4	0.0
Golden-fronted woodpecker	2	0.3	6.3	1	0.3	0.9	10	0.3	30.9	11	0.3	10.2	6	0.3	3.7	3	0.3	3.7	3	0.3	9.6	0	0.3	0.0	7	0.3	22.0	0	0.2	0.0	6	0.3	13.5	0	0.3	0.0	6	0.3	14.3
Golden-olive woodpecker	0	0.3	0.0	0	0.2	0.0	1	0.3	3.5	0	0.3	0.0	1	0.2	4.2	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.2	0.0	0	0.3	0.0	0	0.3	0.0	0	0.3	0.0
Great kiskadee	1	0.4	3.2	3	0.4	2.5	1	0.4	3.2	10	0.4	8.4	2	0.4	6.5	1	0.4	0.8	4	0.4	12.9	0	0.4	0.0	2	0.4	6.5	1	0.3	1.1	4	0.4	9.7	0	0.4	0.0	1	0.4	2.4
Great-tailed grackle	16	0.2	175.4	1	0.2	0.4	2	0.2	23.3	1	0.2	0.4	2	0.2	20.8	11	0.2	4.4	19	0.2	199.6	4	0.3	1.5	5	0.2	55.0	15	0.2	0.4	2	0.2	111.9	3	0.2				

**Table C.3** Counts (C), areas surveyed (A) and densities (D) of tree species in baseline and traditional ranch sites. Species marked with an asterisk (\*) are non-native.

Species	Baseline sites															Traditional ranches																				
	1			2			3			4			5			1			2			3			4			5			6			7		
	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D			
<i>Acacia pennatula</i>	0	0.6	0.0	1	0.6	1.7	5	0.6	8.3	0	0.6	0.0	0	0.6	0.0	2	1.2	1.7	0	1.2	0.0	9	0.6	15.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	4	1.2	3.3
<i>Acosmium panicum</i>	0	0.6	0.0	4	0.6	6.7	0	0.6	0.0	2	0.6	3.3	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Acrocomia aculeata</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	5	1.2	4.2	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8
<i>Adelia oazacana</i>	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Albizia tomentosa</i>	1	0.6	1.7	0	0.6	0.0	4	0.6	6.7	1	0.6	1.7	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	3	0.6	5.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8
<i>Alseodora amorphoides</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	7	0.6	11.7	0	0.6	0.0	1	1.2	0.8	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Anasin</i>	0	0.6	0.0	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Amorpha</i> sp.*	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Apollanessia paniculata</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Astrocacia tremula</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Bauhinia divaricata</i>	0	0.6	0.0	1	0.6	1.7	0	0.6	0.0	1	0.6	1.7	6	0.6	10.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	2	1.2	1.7
<i>Bauhinia unguilata</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0
<i>Belchinitia</i>	0	0.6	0.0	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Boklunche</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Bourreria pulchra</i>	2	0.6	3.3	0	0.6	0.0	7	0.6	11.7	23	0.6	38.3	12	0.6	20.0	2	1.2	1.7	0	1.2	0.0	14	0.6	23.3	0	1.2	0.0	1	1.2	0.8	7	1.2	5.8	0	1.2	0.0
<i>Brosimum allicestrum</i>	0	0.6	0.0	3	0.6	5.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8
<i>Bursaria schlechtendalii</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Bursaria sinaruba</i>	24	0.6	40.0	80	0.6	133.3	155	0.6	258.3	24	0.6	40.0	96	0.6	160.0	7	1.2	5.8	0	1.2	0.0	27	0.6	45.0	2	1.2	1.7	8	1.2	6.7	37	1.2	30.8	8	1.2	6.7
<i>Caesalpinia guameri</i>	0	0.6	0.0	2	0.6	3.3	26	0.6	43.3	61	0.6	101.7	66	0.6	110.0	0	1.2	0.0	0	1.2	0.0	52	0.6	86.7	0	1.2	0.0	1	1.2	0.8	22	1.2	18.3	0	1.2	0.0
<i>Caesalpinia guatemalensis</i>	0	0.6	0.0	0	0.6	0.0	2	0.6	3.3	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0
<i>Cancha</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Capraria biflora</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Carica papaya</i> *	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Catouchia</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Cecropia peltata</i>	0	0.6	0.0	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Cedrela odorata</i>	0	0.6	0.0	5	0.6	8.3	0	0.6	0.0	0	0.6	0.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Cela pendarunda</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	2	0.6	3.3	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0
<i>Cetinae</i>	0	0.6	0.0	0	0.6	0.0	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Charay</i>	0	0.6	0.0	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Checoche</i>	0	0.6	0.0	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Chilche</i>	0	0.6	0.0	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Chitanche</i>	0	0.6	0.0	2	0.6	3.3	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Chloroleucon mangense</i>	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	5	0.6	8.3	5	0.6	8.3	0	1.2	0.0	0	1.2	0.0	9	0.6	15.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	2	1.2	1.7
<i>Chrysophyllum cainito</i> *	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Chrysophyllum mecianum</i>	19	0.6	31.7	2	0.6	3.3	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Citrus aurantium</i> *	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Cusia flava</i>	0	0.6	0.0	4	0.6	6.7	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Cnidocaulis acuminifolius</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0
<i>Coccoloba barbadensis</i>	4	0.6	6.7	18	0.6	30.0	19	0.6	31.7	44	0.6	73.3	30	0.6	50.0	3	1.2	2.5	2	1.2	1.7	59	0.6	98.3	0	1.2	0.0	0	1.2	0.0	22	1.2	18.3	12	1.2	10



**Table C.4** Counts (C), areas surveyed (A) and densities (D) of tree species in baseline and traditional ranch sites (continued). Species marked with an asterisk (\*) are non-native.

Species	Baseline sites															Traditional ranches																				
	1			2			3			4			5			1			2			3			4			5			6			7		
	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D			
<i>Jatropha gumeri</i>	1	0.6	1.7	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	1	1.2	0.8	3	1.2	2.5	0	1.2	0.0
Ki-lim	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	1	1.2	0.8	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Lactia thannia</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	3.6	5.0	0	1.2	0.0	0	1.2	0.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.8
<i>Laguncularia racemosa</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Leucaena leucacephala</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Lonchoarpus rugosus</i>	17	0.6	28.3	10	0.6	16.7	4	0.6	6.7	10	0.6	16.7	17	0.6	28.3	2	1.2	1.7	0	1.2	0.0	4	0.6	6.7	0	1.2	0.0	1	1.2	0.8	13	1.2	10.8	2	1.2	1.7
<i>Lonchoarpus zuel</i>	0	0.6	0.0	23	0.6	38.3	9	0.6	15.0	24	0.6	40.0	0	0.6	0.0	1	1.2	0.8	0	1.2	0.0	16	0.6	26.7	0	1.2	0.0	1	1.2	0.8	1	1.2	0.8	0	1.2	0.0
<i>Lonchoarpus yucatanensis</i>	0	0.6	0.0	9	0.6	15.0	10	0.6	16.7	89	0.6	148.3	75	0.6	125.0	0	1.2	0.0	0	1.2	0.0	22	0.6	36.7	0	1.2	0.0	0	1.2	0.0	4	1.2	3.3	0	1.2	0.0
<i>Luehea speciosa</i>	1	0.6	1.7	5	0.6	8.3	11	0.6	18.3	6	0.6	10.0	5	0.6	8.3	0	1.2	0.8	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	6	1.2	5.0	2	1.2	1.7
<i>Lysiloma latissilicium</i>	11	0.6	18.3	93	0.6	155.0	37	0.6	61.7	14	0.6	23.3	31	0.6	51.7	8	1.2	6.7	0	1.2	0.0	10	0.6	16.7	0	1.2	0.0	3	1.2	2.5	0	1.2	0.0	5	1.2	4.2
<i>Malpighia emarginata</i>	0	0.6	0.0	1	0.6	1.7	2	0.6	3.3	3	0.6	5.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Malpighia glabra</i>	0	0.6	0.0	3	0.6	5.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Malpighia sp.</i>	0	0.6	0.0	2	0.6	3.3	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Manilkara zapota</i>	0	0.6	0.0	21	0.6	35.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	4	1.2	3.3
Mora	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Mariosousa dolichostachya</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	4	0.6	6.7	2	0.6	3.3	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Melicoccus oliviformis</i>	0	0.6	0.0	0	0.6	0.0	3	0.6	5.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Metopium brownei</i>	2	0.6	3.3	77	0.6	128.3	3	0.6	5.0	0	0.6	0.0	12	0.6	20.0	1	1.2	0.8	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	2	1.2	1.7	4	1.2	3.3
<i>Mimosa albidia</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Mimosa bahamensis</i>	0	0.6	0.0	0	0.6	0.0	17	0.6	28.3	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	2	1.2	1.7
<i>Mossanona depressa</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Neea psychotrioides</i>	1	0.6	1.7	20	0.6	33.3	3	0.6	5.0	7	0.6	11.7	12	0.6	20.0	3	1.2	2.5	0	1.2	0.0	5	0.6	8.3	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	2	1.2	1.7
<i>Neomillspaughia emarginata</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	4	0.6	6.7	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
Parent-of-chac-ne-che	0	0.6	0.0	2	0.6	3.3	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
Paro-de-gas	0	0.6	0.0	3	0.6	5.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Phyllanthus acuminatus</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	3	0.6	5.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
Pilim	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Piscidia piscipula</i>	142	0.6	236.7	24	0.6	40.0	50	0.6	83.3	75	0.6	125.0	82	0.6	136.7	9	1.2	7.5	0	1.2	0.0	87	0.6	145.0	0	1.2	0.0	1	1.2	0.8	26	1.2	21.7	7	1.2	5.8
<i>Pisonia aculeata</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Pithecellobium dulce</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	1	0.6	1.7	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Pithecellobium keyense</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Platymiscium yucatanum</i>	1	0.6	1.7	1	0.6	1.7	5	0.6	8.3	5	0.6	8.3	17	0.6	28.3	1	1.2	0.8	3	1.2	2.5	22	0.6	36.7	0	1.2	0.0	0	1.2	0.0	3	1.2	2.5	0	1.2	0.0
<i>Plumeria obtusa</i>	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Plumeria sp.</i>	0	0.6	0.0	2	0.6	3.3	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
Pochote	0	0.6	0.0	3	0.6	5.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
Pokolche	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
Pomoche	0	0.6	0.0	1	0.6	1.7	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Posteria campechiana</i>	0	0.6	0.0	9	0.6	15.0	0	0.6	0.0	0	0.6	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	0.6	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0
<i>Psidium sartorianum</i>	8	0.6	13.3	0	0.6	0.0	6	0.6	10.0	13	0.6	21.7	4	0.6	6.7	0	1.2	0.0	0	1.2																

**Table C.5** Counts (C), areas surveyed (A) and densities (D) of tree species in silvopastoral, *tecnificado* and maize sites. Species marked with an asterisk (\*) are non-native.

Species	Silvopastoral sites								Tecnicafed sites								Maize sites											
	1		2		3		4		1		2		3		4		1		2		3		4		5			
	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	
<i>Acacia pennata</i>	0	1	2	0.0	0	1	2	0.8	3	1	2	2.5	0	1	2	0.0	0	1	2	0.0	5	1	2	4.2	0	1	2	0.0
<i>Acosmium panicum</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	1	1	2	0.8	0	1	2	0.0	0	1	2	0.0
<i>Acrocomia aculeata</i>	0	1	2	0.0	0	1	2	0.0	15	1	2	12.5	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Adelia oaxacana</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	2	1	2	1.7	0	1	2	0.0
<i>Albizia tomentosa</i>	1	1	2	0.8	1	1	2	0.8	1	1	2	0.8	0	1	2	0.8	0	1	2	0.0	0	1	2	0.0	4	1	2	0.0
<i>Alouardos amorphoides</i>	1	1	2	0.8	0	1	2	0.0	1	1	2	0.8	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	4	1	2	0.0
<i>Anasin</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Annona</i> sp.*	0	1	2	0.0	0	1	2	0.0	4	1	2	3.3	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Apocynum schiedtendaliani</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	10.8	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Ascrostoa tremula</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Bauhinia diorixiana</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Bauhinia ungulata</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Belichiche</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Boklundue</i>	0	1	2	0.0	0	1	2	0.0	2	1	2	1.7	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Bourreria pulchra</i>	4	1	2	3.3	5	1	2	4.2	3	1	2	2.5	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Brosimum alcastrum</i>	0	1	2	0.0	0	1	2	0.0	13	1	2	10.8	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Brosimum schiedtendaliani</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Bursera simaruba</i>	3	1	2	2.5	8	1	2	6.7	20	1	2	16.7	22	1	2	18.3	5	1	2	4.2	7	1	2	5.8	1	1	2	0.8
<i>Caesalpinia guameri</i>	2	1	2	1.7	0	1	2	0.0	10	1	2	8.3	0	1	2	0.0	0	1	2	0.0	5	1	2	4.2	23	1	2	0.0
<i>Caesalpinia gualanensis</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	3	1	2	0.0
<i>Cancha</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Capriaria biflora</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Carica papaya*</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	11	1	2	9.2	0	1	2	0.0
<i>Catouchix</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cecropia peltata</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cecropia adusta</i>	0	1	2	0.0	0	1	2	0.0	1	1	2	0.8	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cela. pendurhama</i>	0	1	2	0.0	0	1	2	0.8	1	1	2	0.8	0	1	2	0.8	0	1	2	0.0	2	1	2	0.0	0	1	2	0.0
<i>Cetintine</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Charay</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cheoche</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Childe</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Chitane</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Chloroleucon mangense</i>	0	1	2	0.0	1	1	2	0.8	0	1	2	0.0	2	1	2	1.7	0	1	2	0.8	0	1	2	0.0	2	1	2	0.0
<i>Chrysophyllum castineo*</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Chrysophyllum mezinum</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Citrus aurantium*</i>	1	1	2	0.8	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Citrus flava</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cnidococcus acornifolius</i>	1	1	2	0.8	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Coccoloba barbadensis</i>	2	1	2	1.7	0	1	2	0.0	10	1	2	8.3	0	1	2	0.0	0	1	2	0.0	3	1	2	2.5	0	1	2	0.0
<i>Cochel</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cochlospermum vitifolium</i>	1	1	2	0.8	0	1	2	0.0	4	1	2	3.3	1	1	2	0.8	0	1	2	0.0	2	1	2	1.7	0	1	2	0.0
<i>Coccoloba nucifera*</i>	0	1	2	0.0	0	1	2	0.0	1	1	2	0.8	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cordia alliodora</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cordia gerascanthus</i>	0	1	2	0.0	5	1	2	4.2	3	1	2	2.5	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cordia</i> sp.	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cornutia pyramidata</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Crotona pata</i>	0	1	2	0.0	1	1	2	0.8	1	1	2	0.8	0	1	2	0.0	0	1	2	0.0	2	1	2	1.7	0	1	2	0.0
<i>Crotona replectifolius</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Crotona satup</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cucupel</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Cupania belizensis</i>	0	1	2	0.0	0	1	2	0.0	1	1	2	0.8	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Dactyloctenium</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Delonix regia*</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Despina</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Diospyros anisifolia</i>	2	1	2	1.7	0	1	2	0.0	3	1	2	2.5	0	1	2	0.0	0	1	2	0.0	3	1	2	2.5	0	1	2	0.0
<i>Diospyros salicifolia</i>	0	1	2	0.0	0	1	2	0.0	1	1	2	0.8	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Diphysa carthagenensis</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Drypetes lateriflora</i>	0	1	2	0.0	0	1	2	0.0	3	1	2	2.5	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Dzidza</i>	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Ehretia tinifolia</i>	1	1	2	0.8	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0	0	1	2	0.0
<i>Eleocharis cycloparum</i>	0	1	2																									

**Table C.6** Counts (C), areas surveyed (A) and densities (D) of tree species in silvopastoral, *tecnificado* and maize sites. Species marked with an asterisk (\*) are non-native.

Species	Silvopastoral sites												Tecnificado sites												Maize sites													
	1			2			3			4			1			2			3			4			1			2			3			4			5	
	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D	C	A	D		
<i>Jatropha gumeri</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	2	1.2	1.7	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0		
Ki-lin	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Lactia thannia</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Laguncularia racemosa</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Leucaena leucocephala</i>	1	1.2	0.8	0	1.2	0.0	3	1.2	2.5	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	8	1.2	6.7	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0		
<i>Lonchocarpus rugosus</i>	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	8	1.2	6.7	0	1.2	0.0		
<i>Lonchocarpus zool</i>	0	1.2	0.0	1	1.2	0.8	9	1.2	7.5	19	1.2	15.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	5	1.2	4.2	0	1.2	0.0		
<i>Lonchocarpus yucatanensis</i>	0	1.2	0.0	3	1.2	2.5	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Luehea speciosa</i>	0	1.2	0.0	0	1.2	0.0	4	1.2	3.3	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Lysidroma latissilium</i>	1	1.2	0.8	0	1.2	0.0	2	1.2	1.7	0	1.2	0.0	2	1.2	1.7	0	1.2	0.0	2	1.2	1.7	0	1.2	0.0	0	1.2	0.0	2	1.2	1.7	0	1.2	0.0	0	1.2	0.0		
<i>Malpighia emarginata</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Malpighia glabra</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Malpighia sp.</i>	0	1.2	0.0	0	1.2	0.0	2	1.2	1.7	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Manilkara zapota</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
Mora	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Mariosousa dolichostachya</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Melicoccus oliviformis</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Metopium brownei</i>	0	1.2	0.0	0	1.2	0.0	2	1.2	1.7	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0		
<i>Mimosa albidia</i>	1	1.2	0.8	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Mimosa bahamensis</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	3	1.2	2.5	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Mossanona depressa</i>	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Nera psychotrioides</i>	0	1.2	0.0	0	1.2	0.0	3	1.2	2.5	6	1.2	5.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	2	1.2	1.7	0	1.2	0.0	0	1.2	0.0		
<i>Neomillspaughia emarginata</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
Parent-of-chac-ne-che	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
Paro-de-gas	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Phyllanthus acuminatus</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
Pilin	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	2	1.2	1.7	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Piscidia piscipula</i>	4	1.2	3.3	1	1.2	0.8	30	1.2	25.0	4	1.2	3.3	14	1.2	11.7	2	1.2	1.7	19	1.2	15.8	0	1.2	0.0	0	1.2	0.0	2	1.2	1.7	28	1.2	23.3	0	1.2	0.0		
<i>Pisonia aculeata</i>	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Pithecellobium dulce</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Pithecellobium keyense</i>	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Platymiscium yucatanum</i>	10	1.2	8.3	1	1.2	0.8	1	1.2	0.8	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0		
<i>Plumeria obtusa</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Plumeria sp.</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
Pochote	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
Pokolche	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	5	1.2	4.2	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
Pomoche	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Posteria campechiana</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0		
<i>Psidium sartorianum</i>	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	0	1.2	0.0	1	1.2	0.8								

**Table C.7** Counts of dung beetle species in study sites. Sites marked with (†) had one or two traps destroyed by animals and therefore a slightly lower sampling effort. Species marked with an asterisk (\*) are non-native.

	Baseline sites					Traditional ranch sites							Silvopastoral sites				Tecnificado sites				Maize sites				
Species	1†	2	3	4	5	1	2	3	4	5	6	7	1	2†	3	4	1	2	3	4	1	2	3	4	
Ateuchus perezvelai	0	0	5	14	2	0	0	11	0	0	8	0	0	0	2	0	2	0	0	0	0	3	3	0	0
Canthidium pseudopuncticolle	23	168	26	1	24	14	39	35	22	0	37	16	6	0	64	8	8	15	21	2	0	10	0	19	
Canthon cyaneus	8	23	878	1445	628	0	0	177	0	0	28	8	3	0	5	0	1	2	0	1	0	0	0	0	
Canthon euryseis	1886	4596	5432	3041	5549	5	2	5576	0	0	1573	181	0	0	892	36	21	4	83	0	0	127	0	0	
Canthon indigaceus chevrolati	17	0	96	0	0	164	1009	31	3	3840	4414	286	13220	184	3969	238	3514	2232	2012	8405	43	282	4	3337	
Canthon leechi	108	75	698	1789	2246	188	33	2722	66	10	244	151	263	0	195	1014	348	524	185	77	4	294	175	49	
Copris incertus	45	73	57	136	10	46	80	119	43	0	94	29	17	0	3	0	141	4	15	1	0	13	10	0	
Copris laeviceps	200	260	31	258	0	0	1	0	22	2	5	31	4	1	6	20	9	0	22	0	0	30	1	0	
Copris lugubris	4	5	2	21	0	7	1	3	38	39	14	13	95	1	5	1	516	36	51	3	1	4	4	10	
Coprophanaeus corythus	6	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Deltochilum gibbosum sublaeve	2	14	19	89	35	0	0	0	0	7	0	0	1	4	0	0	2	4	0	6	0	1	0	0	
Deltochilum lobipes	7	9	11	17	1	7	1	3	9	2	13	1	3	2	15	3	4	2	7	0	0	1	0	7	
Deltochilum scabriculum scabriculum	57	11	8	71	19	0	0	15	3	0	6	2	3	0	5	4	1	0	0	0	0	3	0	1	
Deltochilum valgum acropylae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Dichotomis amplicollis	4	5	16	15	25	0	0	0	1	1	0	2	5	0	9	0	2	0	0	0	0	0	0	0	
Dichotomis maya	98	1	0	0	0	1	2	4	43	0	3	5	0	0	5	0	6	8	2	2	0	3	9	1	
Digitonthophagus gazella*	0	0	0	0	0	59	10	4	585	0	0	7	23	0	38	3	343	14	9	72	0	6	5	33	
Eurytermus mexicanus	1	0	0	0	0	7	0	0	0	0	5	8	1	0	1	5	1	17	6	0	0	0	1	0	
Malagoneilla astyanax yucateca	10	0	22	21	0	4	0	3	0	0	20	1	18	4	12	0	52	0	3	1	0	0	1	1	
Onthophagus batesi	0	0	0	0	0	0	0	0	2	1	13	0	96	0	1	6	0	6	25	13	1	2	0	5	
Onthophagus carphophilus	2	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	
Onthophagus cyclographus	1	123	213	100	322	0	0	0	5	0	224	9	0	0	4	0	0	0	0	0	0	0	77	0	
Onthophagus igualensis	3	35	72	169	1	0	0	842	0	0	59	0	1	0	46	0	60	0	107	0	0	28	0	0	
Onthophagus landolti	740	95	2034	884	135	6064	3403	3376	1736	175	1849	1129	544	506	2429	643	4040	1548	837	481	1126	353	610	659	
Onthophagus longimanus	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Pedariidum maya	1	0	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Phanaeus endymion	0	2	23	15	3	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	
Phanaeus pilatei	191	80	105	58	112	6	0	10	0	10	80	7	3	27	4	1	66	4	0	8	0	1	0	9	
Pseudocanthion perplexus	0	0	0	0	0	7157	2504	1	6360	3	1176	469	2592	1222	6529	34	2225	723	3836	257	321	1140	1463	2592	
Sisyphus mexicanus	5318	0	1721	3615	810	0	0	3460	0	0	674	0	14	0	476	0	0	0	0	0	0	0	0	0	
Uroxys chichianich	1078	529	2516	1659	978	104	7	2668	519	0	929	428	6	15	1370	264	83	79	394	0	0	287	0	5	
Uroxys deavilai	5	326	720	4	127	0	0	0	0	0	0	1	2	13	0	15	0	0	12	0	0	0	0	0	
Uroxys micros	0	353	99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

## C.1 Species richness estimates for study sites

**Table C.8** Observed species richness and richness estimates for birds in each study site.

Site type	Site No.	No. points	Obs. species	Chao1	Chao1 se	Jackknife	Jackknife se
Baseline	1	24	55	86.0	20.90	72.2	4.92
Baseline	2	24	54	58.8	3.91	64.5	4.85
Baseline	3	24	55	63.6	6.54	66.5	3.85
Baseline	4	24	72	85.7	8.04	91.2	5.81
Baseline	5	24	54	58.8	3.91	64.5	4.22
Silvopastoral	1	24	44	53.0	6.55	56.5	4.21
Silvopastoral	2	24	34	68.5	32.00	45.5	4.10
Silvopastoral	3	24	61	77.2	8.70	84.0	6.99
Silvopastoral	4	24	60	76.6	9.28	81.1	7.13
Traditional	1	24	53	84.7	18.20	75.0	8.97
Traditional	2	24	37	67.7	22.40	52.3	5.12
Traditional	3	24	58	73.5	9.65	75.2	6.29
Traditional	4	24	42	50.6	6.54	53.5	4.75
Traditional	5	24	44	59.4	9.87	60.3	5.90
Traditional	6	24	46	51.1	3.81	58.5	4.64
Traditional	7	24	47	54.4	5.38	59.5	4.21
Tecnificado	1	24	42	67.9	16.90	59.2	6.59
Tecnificado	2	24	34	55.6	15.40	48.4	6.22
Tecnificado	3	24	36	39.7	3.19	45.6	3.61
Tecnificado	4	24	17	47.7	38.00	24.7	3.87
Maize	1	24	35	36.7	2.00	40.8	2.35
Maize	2	18	17	40.1	29.40	23.6	3.17
Maize	3	24	46	69.1	15.40	62.3	6.80
Maize	4	24	24	31.7	7.19	31.7	4.34
Maize	5	24	32	72.5	36.90	44.5	4.43

**Table C.9** Observed species richness and richness estimates for trees in each study site. Italicised values for one site are show a richness estimate that I feel is unlikely, given the observed richness.

Site type	Site No.	No. points	Obs. species	Chao1	Chao1 se	Jackknife	Jackknife se
Baseline	1	10	38	74.4	25.8	54.2	7.1
Baseline	2	10	77	149.0	32.3	115.0	14.6
Baseline	3	10	44	67.0	16.2	58.4	5.6
Baseline	4	10	50	73.2	14.6	67.1	7.8
Baseline	5	10	57	107.0	27.9	82.2	9.9
Traditional	1	20	25	42.4	11.7	40.2	12.1
Traditional	2	20	7	11.3	6.8	9.8	2.9
Traditional	3	10	40	56.5	11.1	54.4	5.6
Traditional	4	20	8	15.6	11.1	11.8	2.7
Traditional	5	20	20	55.6	28.2	34.2	6.6
Traditional	6	20	40	61.4	13.3	58.0	7.3
Traditional	7	20	36	70.9	21.7	56.0	8.9
Silvopastoral	1	20	28	58.8	20.8	45.1	8.4
Silvopastoral	2	20	16	84.4	79.4	27.4	3.8
Silvopastoral	3	20	48	82.6	18.2	73.6	9.9
Silvopastoral	4	20	45	94.5	29.1	68.8	8.7
Tecnificado	1	20	20	80.8	53.2	35.2	12.8
Tecnificado	2	20	5	5.2	0.5	6.0	1.0
Tecnificado	3	20	22	35.7	10.7	33.4	6.6
Tecnificado	4	20	5	10.7	6.7	8.8	3.9
Maize	1	20	7	16.5	9.6	11.8	2.5
Maize	2	20	22	<i>202.0</i>	<i>82.9</i>	41.0	19.5
Maize	3	20	29	56.5	18.9	45.2	7.0
Maize	4	20	0	<i>NA</i>	<i>NA</i>	<i>NA</i>	<i>NA</i>
Maize	5	20	4	6.8	4.1	6.8	1.6

**Table C.10** Observed species richness and richness estimates for dung beetles in each study site. Note there are only 24 sites, as we were refused permission for one intensive maize site. Number of points refers to the number of intact traps after accounting for those destroyed by animals.

Site type	Site No.	No. points	Obs. species	Chao1	Chao1 se	Jackknife	Jackknife se
Baseline	1	23	25	28.80	5.080	28.80	1.91
Baseline	2	25	20	21.90	3.600	21.90	1.94
Baseline	3	25	24	24.50	1.280	25.00	0.96
Baseline	4	25	22	22.20	0.521	23.00	0.96
Baseline	5	25	20	27.70	11.200	23.80	1.92
Silvopastoral	1	25	20	21.10	1.710	22.90	1.66
Silvopastoral	2	24	10	12.20	3.270	12.90	1.66
Silvopastoral	3	25	23	25.90	4.410	25.90	1.66
Silvopastoral	4	25	17	18.50	2.090	20.80	2.37
Traditional	1	25	14	15.00	2.200	15.90	1.36
Traditional	2	25	12	24.00	16.500	16.80	2.55
Traditional	3	25	19	20.00	1.810	20.90	1.36
Traditional	4	25	17	21.30	6.920	19.90	2.16
Traditional	5	25	9	9.96	1.810	10.90	1.36
Traditional	6	25	25	25.00	0.000	25.00	0.000
Traditional	7	25	21	23.60	3.360	24.80	1.92
Tecnificado	1	25	21	25.00	4.700	25.80	3.51
Tecnificado	2	25	15	16.00	1.810	16.90	1.36
Tecnificado	3	25	18	18.10	0.367	19.00	0.96
Tecnificado	4	25	12	14.20	3.270	14.90	1.66
Maize	1	25	7	11.30	6.920	9.88	2.16
Maize	3	25	17	29.00	16.500	21.80	2.91
Maize	4	25	11	15.30	6.920	13.90	1.66
Maize	5	25	13	15.20	3.270	15.90	2.16

**Table C.11** Observed species richness and richness estimates for all taxa in each site type.

Taxa	Site type	No. sites	Obs. species	Chao1	Chao1 se	Jackknife	Jackknife se
Birds	Baseline	5	90	99	5.6	100	9.2
Birds	Traditional	7	90	100	7.3	110	12.0
Birds	Silvopastoral	4	80	90	5.6	96	10.0
Birds	Tecnificado	4	55	79	14.0	71	11.0
Birds	Maize	5	56	72	9.9	71	12.0
Trees	Baseline	5	125	230	36.0	180	36.0
Trees	Traditional	7	73	100	14.0	100	13.0
Trees	Silvopastoral	4	74	100	12.0	100	20.0
Trees	Tecnificado	4	33	59	16.0	50	12.0
Trees	Maize	5	41	72	16.0	63	17.0
Dung beetles	Baseline	5	30	33	4.0	34	2.8
Dung beetles	Traditional	7	28	30	2.3	31	2.2
Dung beetles	Silvopastoral	4	26	28	2.0	30	3.4
Dung beetles	Tecnificado	4	23	25	2.7	26	2.6
Dung beetles	Maize	4	21	23	2.0	26	3.1